FOREWORD

Most of this issue of *Limnology and Oceanography* is devoted to a single paper, "An experimental approach to the production dynamics and structure of freshwater animal communities," by Hall, Cooper, and Werner. We are printing this long paper not as the beginning of a new publication policy but because it describes a kind of ecosystem study that is becoming increasingly frequent; in this case, done on a relatively small scale, under relatively favorable circumstances. Some ecologists, including the present authors, believe that the detailed study of whole communities and whole ecosystems will divulge properties not evident from studies of their parts, and that these properties will in turn enable the formulation of new theory. Such expanded investigations require support at a high level, like that, for example, currently being provided for part of the International Biological Program. They will eventually require arrangements for publication that most journals as presently organized cannot meet without imposing impossible tasks on referees and displacing large quantities of other material. We present this paper so that our readers may consider such problems in the light of an example of the results of this kind of work.

THE EDITOR

AN EXPERIMENTAL APPROACH TO THE PRODUCTION DYNAMICS AND STRUCTURE OF FRESHWATER ANIMAL COMMUNITIES[1]

Donald J. Hall,[2,3]

Division of Biological Sciences, Cornell University, Ithaca, New York

William E. Cooper, and Earl E. Werner

Department of Zoology, Michigan State University, East Lansing

ABSTRACT

The effects of three levels of inorganic nutrients and two predator densities on aquatic animal communities were examined in a series of twenty 0.07-ha freshwater ponds. The treatments were cross-classified in a randomized block design and continued over 3 years. Analyses of the responses include community composition, secondary production, and demographic description of the dominant species of both zooplankton and benthos. The fish populations and their feeding behavior are described in detail. Ancillary data on water chemistry and primary production were available.

Nutrients generally increased production of the zooplankton but had little effect on community composition. Fish predation had profound effects on the diversity and size distribution of the zooplankton but only affected production at lower nutrient levels. The benthos responded markedly to nutrients during the first year, but this was not apparent the second and third years. The response of the benthos to both nutrients and predation was best shown by changes in the distribution of body size. Both zooplankton and benthic communities showed complementary responses between large- and small-bodied organisms. Differences in the physical structure of the environment (i.e., macrophytes) also produced significant changes in production and composition of both systems. The biomass production of the fish populations was clearly related to nutrient level. Both fish and invertebrate predators were size selective, but the fish had a much greater influence on the prey populations.

INTRODUCTION

A large body of ecological theory centers around the recurrent patterns of species arrays in natural communities (Brookhaven National Laboratory 1969). Empirical derivations have provided a basis for arguments ranging from the definition of communities to models of community evolution and stability. Implicit in most of these arguments is the tenet that the structure of the community is related to the manner in which functional properties are partitioned between the species or species groups. Presumably, then, the resultant assemblages attain relative temporal stability.

Several recent experiments have provided insight into properties important in governing the structure of communities (Paine 1966, 1969; Simberloff and Wilson 1969). The emerging theory of community structure and its resultant evolutionary implications (Levins 1968; MacArthur and Wilson 1967; Margalef 1968) require a continuing input of experimental and descriptive data for sound growth. Of particular interest is
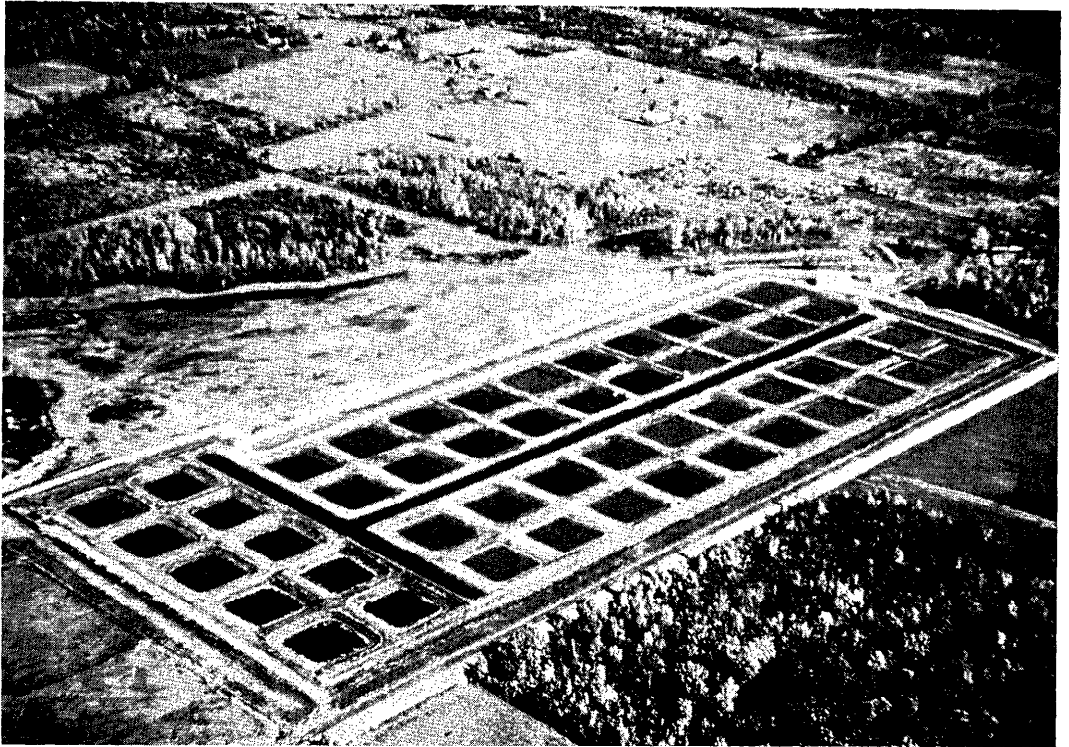
Fig. 1.   Aerial view of Cornell Experimental Ponds Site No. 2 with the reservoir temporarily emptied (center-left). The 20 ponds used in this study lie between the reservoir and the base of the T-shaped feeder canal. (Photograph supplied by S. W. Fertig.)

the relation of patterns in community parameters to the patterns of species population responses. A significant part of community theory rests on the analysis of the interaction of parameters used to describe the dynamics of populations. Generally this has started with notions of the niche or competition and been extended through use of the Lotka-Volterra equations (MacArthur 1968; Vandermeer 1970). Such theory can be of only limited use until further properties emergent at the community level are introduced in the formulations.

We have examined the structural dynamics of aquatic invertebrate communities and a fish population under experimental perturbation. We hoped that changes induced in community structure would indicate what interactions at this level are critical to the construction of a general theory. The apparent significance of nutrients and predation in aquatic systems

prompted us to select these as the parameters most likely to create meaningful changes.

A unique set of replicated ponds at Cornell University allowed us to design and execute a large-scale field manipulation of relatively contained ecosystems. The study was carried out over a 3-yr period. We were able to investigate the zooplankton, benthos, and fish; ancillary data were obtained on the water chemistry and flora of the ponds. The initial objective was to evaluate the impact of simultaneous manipulation of nutrient concentrations and invertebrate predator densities on the zooplankton and benthos. We also wanted to contrast the roles of invertebrate and fish predation.

We have tried to incorporate the advantages of controlled, replicated experimentation and a broad coverage of the community with demographic analysis of

TABLE 1. *Distribution of treatments* between 20 ponds*

1965 and 1966
Block I

Pond No.	21	22	23	24	25	26	27	28	29	30
Treatment	MN	LN	HN	HN	MN	LN	C	MN	MN	LN
Combination	HP	HP	LP	HP	LP	LP		HP	LP	HP

Block II

Pond No.	40	39	38	37	36	35	34	33	32	31
Treatment	LN	MN	HN	LN	MN	HN	C	HN	HN	LN
Combination	HP	HP	HP	LP	LP	LP		HP	LP	LP

Block III

1967
Block I

Pond No.	21	22	23	24	25	26	27	28	29	30
Treatment	MN	LN	HN	HN	MN	LN	C	MN	MN	LN
Combination	WF	WF	WF	F	F	F		WF	F	WF

Block II

Pond No.	40	39	38	37	36	35	34	33	32	31
Treatment	LN	MN	HN	LN	MN	HN	C	HN	HN	LN
Combination	F	F	WF	WF	WF	F		F	WF	F

Block III

* HN—high nutrient   LP—low predation
MN—medium nutrient   HP—high predation
LN—low nutrient   WF—without fish
C—control   F—fish

change in the constituent populations. The broad scope of the study perforce limited the resolution we could provide on details of the causal relationships behind important changes. Our goal was to set the stage for more extensive investigation of specific interactions.

We view this study as essentially a pilot experiment to explore the utility of controlled manipulation of ecosystems in revealing ecological relations that may not be discovered by more conventional studies.

EXPERIMENTAL DESIGN

Identical ponds, in two rows of 10 each, built by the Department of Agronomy, Cornell University, served as the experimental units (Fig. 1). The ponds were constructed on a hardpan clay base with earthen dikes. Each unit has a surface area of 0.07 ha when filled to a depth of 1.3 m. The dikes slope in from the edges about 3 m to a level, 0.04 ha bottom; the volume is about 650 m³. A constant water level was maintained throughout the experiments with water from an excavated upland swamp supplied through a trickle filter to a holding canal and then siphoned to the ponds. The ponds were filled 2 years before our experiment and had a well-developed flora and fauna.

We incorporated 18 of these ponds in a randomized block design (Table 1). In 1965 and 1966, three nutrient levels, high, medium, and low (HN, MN, and LN), and two invertebrate predation levels, high and low (HP and LP), were cross-classified in each of the three blocks. In 1967, verte-

brate predation was substituted for the invertebrate treatment; the nutrient treatments remained unchanged. Fish populations were introduced in 3 of the ponds in each block, one at each food level. Four of the ponds receiving fish were formerly HP and the other five were LP. It is doubtful that the change in design confounded fish and invertebrate predation. We found during the first 2 years that the maintenance of different levels of invertebrate predation required frequent attention throughout summer, or the populations quickly returned to their normal levels. When fish were introduced, the major invertebrate predators declined rapidly; by contrast, the invertebrate predators were abundant in ponds with no fish. During all 3 years, the 2 ponds not included in the design were considered controls, receiving no treatment whatsoever.

The sampling regime provided for duplicate zooplankton and triplicate benthos collections (subsamples) from each pond every week. For the zooplankton, treatment means for a given date were computed from 12 samples each (6×2) at IIN and MN levels. LN (no nutrient addition) means were based on 16 samples since the 2 control ponds could be included here. Predation level and interaction means (not including the control ponds) were computed on the basis of 18 and 6 samples respectively. Similarly, in the benthos, means were obtained from 18 (6×3), 18, and 24 samples for IIN, MN, and LN ponds. Predation means include 27 samples per week and the interaction means 9. Insect emergence rates were estimated from 2 samples per pond; these means accordingly contain 16 samples at LN and 12 at MN and IIN.

The standard errors presented in association with treatments means are calculated from the means of individual ponds since the area sampled is a small fraction of the total pond area (Cochran 1963). These error terms contain several sources of variation. Particularly in the zooplankton, a large component of the variation was the result of asynchrony in population trends.

Short generation times permitted rapid fluctuations in population size. These fluctuations were seldom in phase between the ponds at any treatment level. Also, replicate ponds did not respond synchronously to a given treatment. This affected both the zooplankton and benthos. There appears to be no appropriate way of adjusting the time scale to eliminate these problems. There were also apparent differences in baseline fertility between the ponds at a single treatment level, which contribute to this variation. The randomized block design was used to isolate the effects of an observed gradient in soil type. Generally ponds in block II were less productive than the others. All of these sources of variation are confounded in the error terms with the background sampling variance. Standard errors when given in a figure legend represent the mean error term over the period of the graph.

Some of the reasons for the large variances found are indicated above. Such problems severely limit the utility of conventional testing procedures. In addition, the nonindependence of consecutive estimates of populations precludes the use of standard statistical techniques on our data. The degree of autocorrelation in the samples is a function of generation time and varies with each species. This is, of course, a much more serious problem in the benthos where generation times are considerably longer. Most of the data were evaluated by examination of trends in the mean response of treatment levels. Only the production data were subjected to an analysis of variance. A seasonal total, obtained by summing the weekly production estimates over the sampling period, was used in the analysis. All factors (including the blocking) were considered fixed effects giving the following model:

$$X_{ijkl} = \mu + \alpha_j + \beta_k + \gamma_l + \alpha\beta_{jk} + \alpha\gamma_{jl} + \beta\gamma_{kl} + \alpha\beta\gamma_{jkl} + \epsilon_{ijkl},$$

where

X_{ijkl} = sample mean;

μ = population mean;

α_j = nutrient effect, $j = 1 - 3$;

β_k = predation effect, $k = 1 - 2$;

γ_l = block effect, $l = 1 - 3$;

ϵ_{ijkl} = random error.

Since the $\alpha\beta$ combinations were not repli-cated within blocks, $\alpha\beta\gamma$ and ϵ are con-founded so that the $\alpha\beta\gamma$ interaction must be used as the testing term. When none of the two-way interactions with blocks was significant, a pooled error term based on 10 df was used.

The results are presented as two discrete experiments: the nutrient–invertebrate ma-nipulations (1965–1966) and the nutrient-fish experiment (1967). The zooplankton and benthos are analyzed separately, gener-ally according to the response to nutrients, to predation, and finally to the interaction of nutrients and predation. Four basic types of data are given: total standing crop biomass of the community, the species composition according to biomass (a mea-sure of diversity), biomass production, and counts of the dominant species. Although they are interrelated, each reveals impor-tant aspects of community structure. Fi-nally the zooplankton and benthos data are combined to evaluate the composite re-sponse. A detailed analysis of the fish populations adds a further dimension to the 1967 results.

MANIPULATIONS 1965, 1966

Nutrients

Commercial fertilizers (urea, superphos-phate, and potassium chloride) were mixed to a $10:1:1$ ratio of $N:P:K$, which ap-proximates the elemental ratio in many organisms. The 6 HN ponds each received 2.72 kg of this mixture per week, the 6 MN ponds received 0.23 kg/week, and the 8 control or LN ponds received no fertilizer at all. These quantities were chosen to generate a wide range of conditions from an unproductive control to a maximal pro-duction level, but still falling short of cre-ating anoxic conditions. Nutrients were added semiweekly from 16 June to 20 August 1965 and from 10 June to 24 August 1966 by dissolving the fertilizer in pails
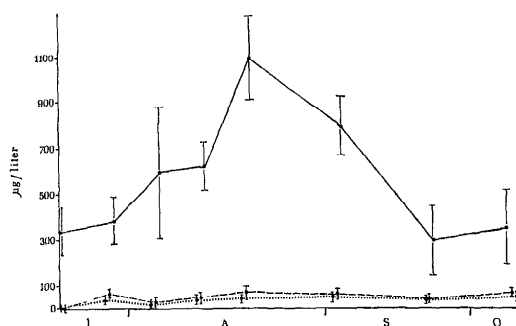

FIG. 2. Mean concentrations of NH_3-N $\pm$ 1 SE at three nutrient levels in 1965 (HN ——, MN – – –, LN $\cdots$).

and broadcasting it from all sides of the ponds.

The experimental period was limited to summer months to avoid the possibility of winterkill (anoxic conditions) and the massive spring growth of blue-green algae typical of many fertilized ponds.

Water samples for nutrient analysis were collected the day before fertilizer applica-tion, 0.3 m below the surface in the center of the pond. Analyses for ammonia, nitrate, and phosphate were made according to Strickland and Parsons (1960). Total phos-phorus was determined by the persulfate oxidation method (Menzel and Corwin 1965). A galvanic cell-thermistor probe was used to monitor oxygen and temperature at the surface and bottom of the ponds each week between 0700 and 1000 hours. Total alkalinity was determined by 50 N acid titration and a pH meter.

Since our experimental design was based on establishing three discrete nutri-ent levels and two predator densities, the responses to these are reported next. Am-monia concentrations (Fig. 2) were much higher in both years in the HN ponds than in the MN and LN ponds, which showed no differences. Concentrations in the HN ponds increased until fertilization ceased in late August. Nitrate concentrations were usually very low or undetectable. Reactive-phosphorus concentrations (Fig. 3) were also highest in HN ponds, with no differ-ences between MN and LN ponds. Total
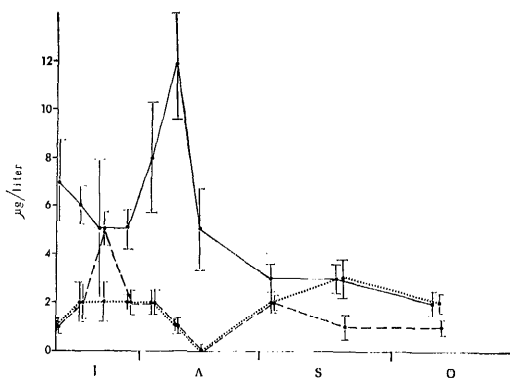
FIG. 3. Mean concentrations of PO_4-P $\pm$ 1 SE at three nutrient levels in 1965 (IIN ——, MN – – –, LN $\cdots$).

FIG. 4. Mean near-bottom pond temperatures.

(unfiltered) phosphorus revealed the same pattern.

The mean summer alkalinity was 54 and 59 mg/liter $CaCO_3$ in 1965 and 1966. In both years, alkalinity in block II averaged ~5 mg/liter lower than in the other blocks. Oxygen was uniformly high (>8 mg/liter) in all ponds at both surface and bottom except in ponds 23 and 24 during a bloom of *Oocystis pusilla* in August 1965. Temperature varied little between ponds or years (Fig. 4). Maximum afternoon temperatures rarely exceeded 28C, and minimum temperatures were usually above 20C.

In 1965, Mulligan (1966) studied the phytoplankton in 10 of the 20 ponds. Weekly samples were counted as described by Mulligan and Kingsbury (1968). Included in these 10 ponds were 3 HN, 2 MN, and 5 LN levels. The HN ponds contained 26 ± 1.8 ($\overline{X} \pm$ SE) species whereas the MN and LN ponds contained 29 ± 2.8 and 34 ± 1.9 species. The mean summer dry weight of seston from these ponds was: HN—9.5 ± 6.9; MN—2.3 ± 0.2; and LN—1.8 ± 0.3 mg/liter. The summer phytoplankton was dominated by members of the Chlorococcales (*Scenedesmus* spp., *Oocystis pusilla*, *Pediastrum boryanum*, and *Tetrahedron minimum*). Other abundant species were *Eudorina elegans*, *Pleodorina californica*, *Pandorina morum*, *Euglena* spp., *Glenodinium* spp., *Volvox*, and occasionally *Ceratium hirundinella*. Cyanophyta and
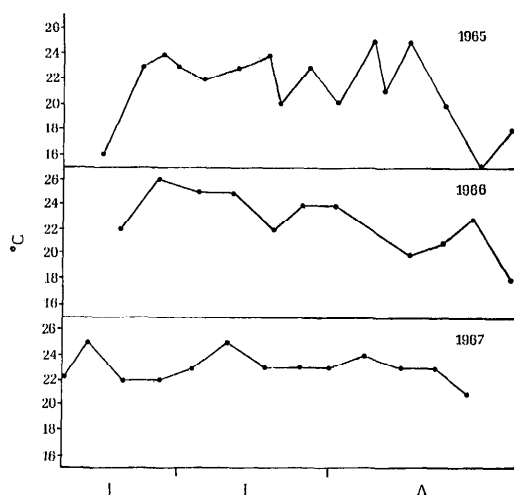
desmids were rare. Phytoplankton samples were unavailable in 1966.

Chlorophyll *a* samples were collected weekly in 1965.[4] One liter or less of water was passed through a glass filter which was then ground in a tissue blender containing 90% acetone. After centrifugation, sample volumes were made up to 10 ml and pigment concentrations determined with a D-U2 spectrophotometer. Results are expressed according to the Parsons-Strickland equation. The highest chlorophyll concentration occurred in the HN ponds; MN and LN ponds were again similar (Table 2). Concentrations in HP and LP ponds showed no differences.

Primary productivity was measured by the ^{14}C technique on 6 dates in 1966. All 6 ponds in a given block were sampled on the same day. Each pond was sampled twice during the summer. A pair of 250-cc light and dark bottles was suspended at 0.3 and 0.6 m from 0900–1300 hours, with 5 μCi of ^{14}C-$NaHCO_3$ in each. Samples were filtered under low vacuum, acid-rinsed, desiccated, and counted by liquid scintillation. Above pH 9.5, the correction technique of Saunders, Trama, and Bach-

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[4] Most of the chlorophyll data in this study were supplied by Dr. H. Mulligan, Department of Agronomy, Cornell University.

TABLE 2. *Summer phytoplankton chlorophyll a concentrations (mg/m³) in 1965 and carbon assimilation rates (mg C m⁻³ 4 hr⁻¹) using the ¹⁴C technique in 1966*

	Chl a $\bar{X} \pm$ SE $n = 7$ dates	¹⁴C $\bar{X} \pm$ SE $n = 6$ dates
Nutrient level		
HN	55.5 ± 18.67	282 ± 87.4
MN	6.0 ± 0.88	34 ± 5.1
LN	2.9 ± 0.53	28 ± 4.8
Predation level		
HP	24.4 ± 6.14	140 ± 64.3
LP	37.2 ± 12.50	88 ± 27.4

TABLE 3. *Benthic flora survey, 1966, illustrating the mean number of quadrats (from a total of 340) with specific dominant forms*

	D*	Chara	Eleocharis	Filamentous algae	Other†
			Early July 1966		
LN	0–1.8	173.40	33.62	1.99	8.90
	>1.8	91.37	0.0	0.12	1.15
MN	0–1.8	86.50	22.83	9.49	6.46
	>1.8	79.50	0.0	0.0	3.40
HN	0–1.8	1.50	10.50	76.66	11.20
	>1.8	0.33	0.0	40.32	6.86
			Late August 1966		
LN	0–1.8	82.62	57.62	0.0	8.40
	>1.8	31.25	0.62	0.0	2.93
MN	0–1.8	13.00	21.33	11.67	6.10
	>1.8	19.50	0.12	1.83	0.93
HN	0–1.8	1.66	19.17	69.84	10.13
	>1.8	0.0	0.0	22.66	4.80

* Linear distance from the edge of the pond in meters.
† Others include: *Najas, Potamogeton, Elodea, Typha,* and *Juncus.*

mann (1962) was followed. The averaged results in Table 2 compare uptake rates at the three nutrient conditions. Again, HN ponds showed the highest production rates and MN and LN ponds did not differ. There was no predator effect.

Three surveys were made of the macroscopic plants, one in 1965 and two in 1966. The shoreline of each pond was divided into 17 sections (each 1.5 m). The dominant species, determined by a relative cover index, were recorded in each section at distances of 0.6, 1.8, 2.4, and 3.0 m from shore. The survey in August 1966 used distances of 0.3, 0.6, 0.9, 1.2, and 1.5 m, since visibility was often restricted to 1.5 m. In each pond, data from 340 quadrats were recorded. If a quadrat contained two dominant forms, both were noted (thus often giving more than 340 observations per pond).

Table 3 presents the data from the 1966 surveys. *Chara* and *Eleocharis* were the dominant forms at LN and MN levels; the *Eleocharis* being restricted to the very edge of the ponds. The HN ponds contained almost no *Chara*, and filamentous algae (*Rhizoclonium* and *Spirogyra*) dominated the benthic flora. Results from the 1965 survey were similar.

Invertebrate predators

High and low predator densities were established by hauling a 30.5 m long, 3-mm-mesh seine through the 9 LP ponds (three

replicates within each of the three nutrient levels). Ponds were seined at 1- or 2-week intervals at night during summer. Predators removed from LP ponds were placed in HP ponds within the same block in a systematic fashion to ensure a fairly uniform density within treatment levels. Zooplankton passed through the seine, but benthic herbivores were usually below the path of the net. Any herbivores removed by this manipulation would tend to decrease the anticipated effects of high and low predator densities on prey abundance.

The manipulated predators were: *Buenoa margaritacea, Notonecta undulata,* and *N. insulata* (Hemiptera); *Anax junius, Libellula* sp., and other Odonata. All of these feed voraciously on zooplankton or benthos. Eggs of each species were hatched in the laboratory and cohorts were fed a variety of prey. *Notonecta* and Odonata consumed nearly any prey offered but favored midge larvae. *Buenoa* fed exclusively on zooplankton. The minimum generation times of the predator species were estimated to range from 30 days for *Buenoa, Notonecta, Chaoborus,* and *Laccophyllus* to 60 days for Zygoptera and 90 days for *Anax.* How-
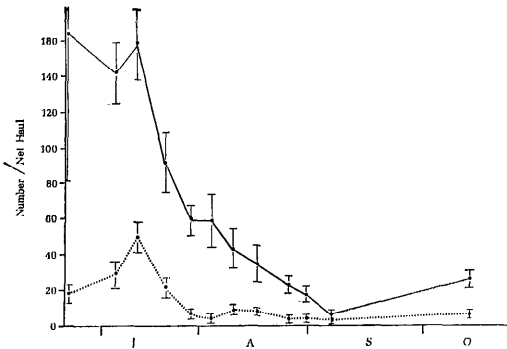
FIG. 5.   Mean numbers of *Buenoa* ± 1 SE/plankton sample at two predation levels in 1966 (HP ——, LP · · ·).

ever, field observations indicated that all major predators had but one or at most two generations per year.

Notonectids were sampled by the plankton net used in the zooplankton study. Weekly estimates of *Buenoa* abundance are plotted in Fig. 5. Eggs hatching in June and early July resulted in a population dominated by early instars. By summer's end the population consisted primarily of late instars and adults. The decreasing numbers reflect both mortality (including cannibalism) and net avoidance. *Notonecta* showed a similar effect.

The total numbers of *Anax junius* collected in emergence traps during summer 1965 were 506 in IIP ponds and 237 in LP ponds. This relationship occurred in each of the three blocks of ponds. Clearly, our manipulations produced two distinctive predator densities.

Chaoborus sp., which passed through the seine, was always more abundant in the LP ponds. This may have been due to greater predation on *Chaoborus* by backswimmers and dragonflies in the HP ponds or to reduced predator competition in the LP ponds.

MANIPULATIONS 1967

Nutrients

Two minor changes were made in the nutrient manipulations in 1967. In previous years the MN level did not show a signifi-

cant response over LN, so the amount of fertilizer added to MN ponds was increased from 0.23 to 0.69 kg per week. The other change was to alter the nitrogen source from 100% urea-N to 90% urea-N and 10% NO_3-N. The ponds were fertilized from 10 June until 24 August.

Total unfiltered phosphorus was the only nutrient measured regularly in 1967. The average concentrations of total phosphorus in summer were: HN = 64 ± 6, MN = 30 ± 2, and LN = 17 ± 2 μg/liter, and HP = 38 ± 6, LP = 37 ± 7. A single set of nitrate determinations revealed mean concentrations of: HN = 2.90 ± 1.295, MN = 0.42 ± 0.061, and LN = 0.25 ± 0.046 μg-atoms/liter. Total alkalinity, averaged over all ponds, was 78.3 ± 3.2 mg/liter, an increase of 19 mg/liter over 1966.

Oxygen and temperature were monitored every week in summer. Bottom oxygen values were always greater than 2 mg/liter except in ponds 23 and 24 which contained dense growths of *Elodea canadensis*. Morning temperatures were extremely uniform, averaging 23C (Fig. 4).

Oxygen, temperature, and pH were measured throughout a 24-hr period on 22 August in 3 very different ponds. HN pond 24 was overgrown with *Elodea*, while HN pond 38 contained a more open and heterogeneous assemblage of vascular plants and filamentous algae. The bottom of LN pond 22 was carpeted with *Chara* spp. The results (Table 4) reveal very different physical-chemical characteristics in the 3 ponds. Pond 24 had a striking diurnal range of pH (8.8–10.1), temperature (19.2–25C), and oxygen (2.6–19.8 mg/liter). Vertical stratification, apparently due to the dense stand of vegetation, resulted in extremely low oxygen values (~1 mg/liter) at the bottom and presumably occurred whenever wind velocities were low or nights remained warm. Pond 38 revealed similar but less striking diurnal fluctuations and stratification. Although oxygen values were relatively low near the bottom (2.6 to 3.8 mg/liter), the pond circulated completely before the next morning. By contrast, pond 22 showed a reverse oxygen stratification

TABLE 4. *Diurnal temperature, oxygen, and pH characteristics of 3 ponds on 22 August 1967*

Time	Depth (m)	No. 38 (HN)			No. 24 (HN)*			No. 22 (LN)		
		Temp (°C)	O₂ (mg/liter)	pH	Temp (°C)	O₂ (mg/liter)	pII	Temp (°C)	O₂ (mg/liter)	pH
0715	0.1	21.8	4.0	8.3	19.2	2.6	9.0	21.0	4.65	8.6
	0.3	21.5	3.8		19.2	2.2		21.0	5.25	
	0.6	21.5	3.8		19.2	1.1		21.0	6.0	
	0.9	21.5	3.8		20.0	2.2		21.0	6.0	
	1.2	21.5	3.8	8.3	20.0	1.0	8.8	21.0	6.0	8.4
1100	0.1	21.1	6.0	8.5	22.1	5.6	9.4	22.0	7.7	8.7
	0.3	21.2	5.5		21.4	5.7		22.0	7.6	
	0.6	21.2	4.8		21.3	5.7		21.1	7.6	
	0.9	21.1	4.3		21.1	4.5		21.0	8.0	
	1.2	21.1	3.5	8.7	20.2	2.2	8.8	21.0	8.6	8.5
1600	0.1	25.4	10.1	9.0	25.0	19.8	9.8	24.4	9.9	8.9
	0.3	25.4	10.3		22.1	11.2		24.1	9.8	
	0.6	23.4	9.4		21.0	6.6		24.1	9.6	
	0.9	22.1	6.1		20.0	4.8		23.3	11.4	
	1.2	21.4	4.1	9.0	19.4	2.2	9.7	23.2	11.6	8.9
2200	0.1	22.2	10.5	9.4	21.4	12.7	10.1	23.0	10.1	9.1
	0.3	22.2	11.3		22.1	12.7		23.2	10.5	
	0.6	22.3	9.2		22.0	5.5		23.2	10.9	
	0.9	22.2	5.7		21.0	1.9		23.2	10.9	
	1.2	22.0	2.6	8.9	20.2	1.4	9.7	23.2	9.3	9.1

* Filled with *Elodea canadensis*.

with midday maxima of 11.6 mg/liter at the bottom. Temperature stratification was ephemeral—a condition typical of the LN and MN ponds.

Phytoplankton was collected from all 20 ponds on several dates with a 0.5-liter jar inverted 0.3 m under the surface. Samples were preserved in Lugol's solution and examined (deNoyelles 1968). Only the 3 August samples were counted, but deNoyelles found both species composition and relative abundance to be similar on other dates. All species were identified except for a miscellaneous category of inscrutable small cells which included some coccoid blue-greens, flagellates, and bacteria.

The average number of species of phytoplankton in the HN ponds was only 6.8 ± 1.19 (SE); in MN and LN ponds the numbers increased to 14.0 ± 1.24 and 11.5 ± 0.60. Diatoms, rare in all samples, were not included. This depauperate array is not surprising in small ponds. The extremely rich periphyton community was

occasionally sampled, but results are not yet available.

The colonial *Pleodorina californica* was abundant in all 6 HN ponds; 2 ponds (32 and 33) were dominated by *Microcystis aeruginosa*, 2 by *P. californica*, and 2 by small flagellates. *Cryptomonas rostrata* and *Scenedesmus quadricata* occurred in 5 of the 6 ponds.

Kirchneriella contorta occurred in 12 of the 14 MN and LN ponds and was dominant in 5 but present in only 1 HN pond. *Chlamydomonas, Chlorella vulgaris, Scenedesmus, Oocystis*, and flagellates were abundant in all the LN and MN ponds. The average standing crop was much higher in the MN ponds (140,140 cells/ml) than in the LN ponds (19,930 cells/ml). Although the preponderance of colonial forms in the HN ponds precludes comparison by cell counts, standing crops were clearly greatest at HN levels. There were no differences in species composition between ponds with and without fish.

TABLE 5. *Mean phytoplankton chlorophyll a concentration (mg/m³) and phytoplankton carbon assimilation (mg C m⁻³ 4 hr⁻¹) using the ¹⁴C technique in summer 1967*

	Chl a $\overline{X} \pm$ SE $n = 6$ dates	^{14}C $\overline{X} \pm$ SE $n = 6$ dates
Nutrient level		
HN	37.9 ± 9.71	994 ± 407.0
MN	13.9 ± 2.42	207 ± 51.8
LN	5.7 ± 0.82	66 ± 11.6
Predation level		
F	19.8 ± 7.52	266 ± 87.1
WF	19.6 ± 5.92	579 ± 284.0

Chlorophyll a samples were taken biweekly. Primary production was estimated by the ^{14}C technique twice during 1967, following the procedure of 1966. Both average chlorophyll concentrations and the pooled primary production rates measured by ^{14}C show large mean differences (Table 5). Although the standard errors are relatively large, the differences strongly suggest a nutrient effect. Again, there were no significant differences between ponds with and without fish.

In 1967, the benthic flora was not surveyed, but the plant material from the Eckman dredge samples was preserved. Dr. B. Moss, Department of Botany and Plant Pathology, Michigan State University, has provided identifications and estimates of dry weight biomass.

The *Chara* and *Elodea* were treated with 0.2 M HCl to correct for $CaCO_3$. All the material was dried at 90C. This mode of sampling is probably adequate only for plants such as *Chara* and the filamentous algae. In addition, the edges of the ponds are not represented since the samples were all taken from the flat bottoms. Despite these limitations, the data agree with those from the previous surveys. *Chara* dominated LN and MN ponds with average dry weight standing crops of 1.047 ± 0.116 g and 1.290 ± 0.183 g per Eckman dredge. Filamentous algae and *Elodea* predominated at HN levels. Similar values (about 1.83 g) for *Chara* were obtained from Eck-

man samples in Sugarloaf Lake, Michigan (Beatty and Hooper 1958).

Fish predation

The fish predation experiment was performed within the structure of the nutrient design. In 1967, 1 pond at each nutrient level was selected from each block to receive fish (Table 1). We wanted a species characteristic of small, warm-water ponds, not cannibalistic, with generalized forage habits encompassing the majority of the pond herbivores. The bluegill sunfish (*Lepomis macrochirus*) was most suitable for our purposes.

To simulate reasonable predation pressures on the prey populations, we had to introduce a density and size structure relevant to field situations. A given energy source can either maintain a relatively large standing crop biomass or support the rapid growth of a lesser stock, with a balance maintained between the biomass of a population, the distribution of that biomass in age or size classes, and the rate at which new material is being produced. We selected a density and size structure that was realistic in terms of natural aquatic ecosystems, included all size categories from fry to adults, and permitted a wide range of individual growth responses.

Estimates of the standing crops of bluegill populations in both natural lakes and farm ponds commonly range from 56 to 112 kg/ha at comparable latitudes. A value of 50 kg/ha of fish 1 year or more in age was selected as the stocking rate. The ponds had 0.07 ha of surface area, so they received about 3.3 kg/pond. We assumed that natural reproduction would provide recruitment early in the summer.

The size structure of the bluegill population in Third Sister Lake, Michigan (Brown and Ball 1942), a natural population with no fishing pressure, was used to compute the size distribution of the proposed populations. This distribution had to be modified subsequently, as some of the size classes were not available to us and the distribution was skewed somewhat to smaller individuals. The fish were stocked

at 1,260/pond according to the size structure given in Table 6.

To ensure as constant a genetic and nutritional history as possible, we got fish from a common hatchery stock at the Federal Fish Hatchery, La Mar, Pennsylvania. Unfortunately, the hatchery was unable to provide us with size class III fish; these were obtained from a single farm pond in the Ithaca area.

Fish from the hatchery were stocked in the Cornell ponds on 27 April 1967. Class III fish were not available until 31 May and were stocked then. In all cases the fish were sorted and counted by hand with random samples taken for size-frequency data. Local holding ponds identical with the experimental ponds received complements of each size class to provide replacement individuals for the summer sampling regime.

ZOOPLANKTON

Methods 1965–1966

Zooplankton samples were collected every week during summer with a 0.3-m-diam No. 20 net mounted on a pole in front of the boat. Vertical movement of the pole caused the net to follow a sinusoidal path. The basic sampling design within ponds was a 3 × 3 grid. From this set of 9 possible pairs of right-angle transects, 1 pair was selected at random for the tows. Each of the 2 transects constituted a subsample (1,870 liters), allowing within-pond variability to be estimated. The average coefficient of variation for duplicate transects in 1965 and 1966 was: *Ceriodaphnia* (dominant crustacean) 18% and *Keratella cochlearis* (dominant rotifer) 24%.

Initially, samples were taken during the daytime, but most of the zooplankton concentrated just at or above the bottom, so from 22 July 1965 onward all sampling was done at night when the vertical distribution of plankton was more uniform.

Zooplankton densities were undoubtedly underestimated since the No. 20 net is less than 100% efficient. To evaluate the magnitude of this problem, we collected a series

TABLE 6. *Initial stocking rate*

	Size class			
	I	II	III	IV
Mean std length (mm)	19.50	35.00	68.00	161.10
Mean dry wt estimate (g)*	0.0385	0.2948	2.7696	49.5100
Frequency	1,000	150	100	10
Class dry wt (g)	38.50	44.22	276.96	495.51
% composition by wt	4.51	5.18	32.48	58.12
% composition by numbers	79.36	11.90	7.93	0.79

* Dry weight estimates obtained from fish collected in fall.

of samples with the tow net, using a 90-liter plankton trap as the reference (O'Brien 1970). Based on 15 comparisons, which included all size classes of plankton, the efficiency of the tow net was $57 \pm 8\%$ ($\overline{X} \pm$ SE). These samples came from both ponds with dense *Volvox* populations and those with a scanty phytoplankton. Schindler (1969) concluded that No. 20 net tows were $64 \pm 13\%$ as efficient as his 29-liter trap. Based on No. 20 net tows over a 90-m course, Cummins et al. (1969) found a sampling efficiency of about 40% using the quotient of meter reading inside/meter reading outside the net. All of the above studies involved 0.3-m-diam nets. In a comparison of the retention of a No. 25 net ($64-\mu$ mesh) to that of the No. 20 net ($76-\mu$ mesh) to determine the sampling efficiency for rotifers, relatively few passed through the No. 20 net and these were infrequently members of the dominant species.

We have used the raw numbers for all analyses since applying a blanket correction factor for net efficiency would not change the trends in the data. A 2-fold correction factor is invoked, however, when we compare zooplankton and benthos production.

Samples were preserved in 70% ethanol and 3% formalin. Normally 2 subsamples (1 ml each) were counted in depression slides under a dissecting microscope. All

rotifers and crustaceans were counted by species. Wherever possible, life-history stages, sex, and number of eggs carried were also recorded. Protozoans were noted but not counted. The ratio of variance to mean of each dominant species in the subsamples did not depart significantly from 1, validating the random subsampling procedure (Hall 1964).

Crustaceans were identified according to Brooks (1959), Wilson (1959), and Yeatman (1959). Rotifers were examined by W. T. Edmondson and J. Gilbert. Five or more replicate samples (25 to 200 individuals) of the abundant crustacean species were weighed with a Cahn Electrogram balance after being oven-dried for 24 hr at 70C and then held 2 hr in a desiccator at room temperature. These weights and others calculated indirectly are listed in Table 7. The distinctions between adult and juvenile crustaceans are based on mean minimum carapace length of egg-bearing individuals.

Results 1965–1966

Nutrients

Total biomass. As the starting point in the analyses, we took total biomass, which integrates the response of some 66 species to the manipulation of food and predation. Total standing crop for each pond in 1965 is given in Fig. 6. Of the 12 LN and MN ponds, 8 were characterized by low standing crops, either decreasing or remaining relatively constant through the season. Ponds 25, 30, 36, and 37 showed moderate fluctuations in early August. The 6 HN ponds demonstrated larger fluctuations and, with the exception of ponds 23 and 24, much higher average standing crops than the LN and MN ponds. The fluctuations showed no synchrony, especially in the HN ponds. In 1966 the biomass in LN and MN ponds often revealed a bimodal pattern with a midsummer trough (Fig. 7), but LN ponds 26 and 31 had high densities and moderate fluctuations. The HN ponds were again characterized by asynchronous fluctuations of striking amplitude (with the exception of 23). Comparisons between

years can only be made for the last half of summer; the standing crop biomass for June and early July 1965 was not estimated because of the bias in the daytime samples.

Figure 8 reflects the mean total biomass response of the three nutrient levels. The positive nutrient effect in 1965 was repeated in similar fashion in 1966, except for the increase in LN ponds. Soon after fertilization ceased in late August, the total biomass in the HN and MN ponds began to decrease until by mid-October all ponds showed low densities.

Community composition. The percent of the biomass contributed by each species of zooplankton was found for each sample from which treatment combination means were calculated. Since rotifers are about two orders of magnitude smaller than *Ceriodaphnia*, and since other crustaceans were relatively rare, the species biomass composition and the body size breakdown are identical. Figure 9 shows the dominance of *Ceriodaphnia* in the zooplankton (60–90% of total biomass) at all three nutrient levels in late July and August 1965. Relative contributions were almost identical even though there was a 6-fold difference in mean total biomass between HN and LN ponds. Total rotifers, excluding the large, predaceous *Asplanchna*, treated separately, contributed little to the total biomass (2–18%) until September and October, by which time the biomass of the zooplankton community had greatly diminished. "Other" species included copepods and occasional cladocerans, none of which exceeded a few percent of the total.

In 1965, *K. cochlearis* and *Polyarthra* sp. accounted for 76 ± 3% of the total number of rotifers represented by the 39 identified species. These two species also dominated the total rotifer biomass. Thus, not only was the entire zooplankton community dominated by a relatively large plankter, *Ceriodaphnia*, but within the smaller size category, two species of rotifers dominated both in numbers and in biomass.

Ceriodaphnia maintained its dominance in 1966, composing 40–80% of the total

TABLE 7. *Zooplankton species list and dry weights* (µg)

Cladocera (17 species)		
Acroperus harpae	a*	6.0
Baird 1843	j	3.0
Alona costata	a	3.0
Sars 1862	j	1.0
A. guttata	a	1.8
Sars 1862	j	1.0
Bosmina longirostris	a	1.8†
(O. F. Müller) 1785	j	1.0
Camptocercus rectirostris	a	5.0
Schødler 1862	j	2.0
Ceriodaphnia reticulata	a	4.2†
(Jurine) 1820	j	2.2†
Chydorus sphaericus	a	2.0†
(O. F. Müller) 1785	j	1.0
Daphnia pulex	a	35.0†
Leydig 1860	j	8.0
Diaphanosoma brachyurum	a	7.0†
(Lieven) 1848	j	3.0
Eurycercus lamellatus	a	80
(O. F. Müller) 1785	j	10
Leydigia acanthocercoides	a	6.0
(Fischer) 1854	j	3.0
L. quadrangularis	a	6.0
(Fischer) 1854	j	3.0
Macrothrix laticornis	a	2.0
(Jurine) 1820	j	1.0
M. rosea	a	2.0
(Jurine) 1820	j	1.0
Pleuroxus denticulatus	a	2.0
Birge 1878	j	1.0
P. procurvis	a	4.0
Birge 1878	j	2.0
Simocephalus serrulatus	large a	66.2†
(Koch) 1841	small a	33.5†
	j	8.5†

Copepoda (10 species)	
Calanoid copepodids	3.0
Cyclopoid copepodids	3.0
Cyclopoid nauplii	1.0 × 10⁻²
Cyclops vericans rubellus	
Lilljeborg 1901	2.0
Cyclops vernalis	
Fischer 1853	8.6†
Diaptomus leptopus	
S. A. Forbes 1862	20
D. pallidus	
Herrick 1879	8.1†
Eucyclops agilis	
(Koch) 1838	8.0
Macrocyclops albidus	
(Jurine) 1820	40.0
Mesocyclops edax	
(S. A. Forbes) 1891	18

M. leuckarti	
(Claus) 1857	15
Paracyclops fimbriatus poppei	
(Rehberg) 1880	3.0
Tropocyclops prasinus	
(Fischer) 1860	3.0

Rotifera (39 species)	
Ascomorpha sp.	4 × 10⁻²
Ascomorphella sp.	
Asplanchna girodi	
de Guerne 1888	1.0
A. priodonta	
Gosse 1850	2.0
Brachionus angularis Grosse 1851	
B. plicatilis	
O. F. Müller 1786	6 × 10⁻²
B. quadridentatus Hermann 1783	
Collotheca sp.	
Colurella bicuspidata (Ehrb.)	
Conochilis sp.	
Euchlanis incisa Carlin 1939	
Filinia pejleri Hutchinson	
Gastropus stylifer Imhof 1891	
Gastropus sp.	5 × 10⁻²
Hexarthra reducens Bartos	
Keratella cochlearis (Gosse) 1851	5 × 10⁻³
K. earlinae	
K. hiemalis Carlin 1943	5 × 10⁻³
K. quadrata (O. F. Müller) 1786	
Lecane elasma	
Harring and Myers 1926	
L. luna (O. F. Müller) 1776	
L. ohioensis (Herrick) 1885	
Lepadella ovalis	
(O. F. Müller) 1786	
L. patella	
(O. F. Müller) 1786	
Monostyla bulla (Gosse) 1886	
M. cornuta (O. F. Müller) 1786	
Monostyla lunaris (Ehrb.) 1832	
M. quadridentata (Ehrb.) 1832	
Mytilina mucronata	
(O. F. Müller) 1773	
Platyius patulus (O. F. Müller)	
P. quadricornis (Ehrb.)	
Polyarthra sp.	5 × 10⁻²
Pseudoploesoma formosa	
(Myers) 1938	
Stephanoceros fimbriatus Ehrb. 1832	
Synchaeta pectinata Ehrb. 1832	0.2
Trichocerea cylindrica (Imhof) 1891	
T. longiseta (Schrank) 1802	
T. similis	
T. tetractis	

* a = Adult; j = juvenile.

† Direct dry weights; all other crustacean dry weights were obtained from volume estimates multiplied by a specific gravity of 1.025 (Luntz 1928). All rotifers without dry weight estimates were assumed to weigh 1×10^{-2} µg. Dry weights for rotifers were obtained by multiplying volumes (Nauwerk 1963) times 1.025.

LOW NUTRIENT   MEDIUM NUTRIENT   HIGH NUTRIENT

125 µg/ l   250 µg/ l   500 µg/ l

ZOOPLANKTON
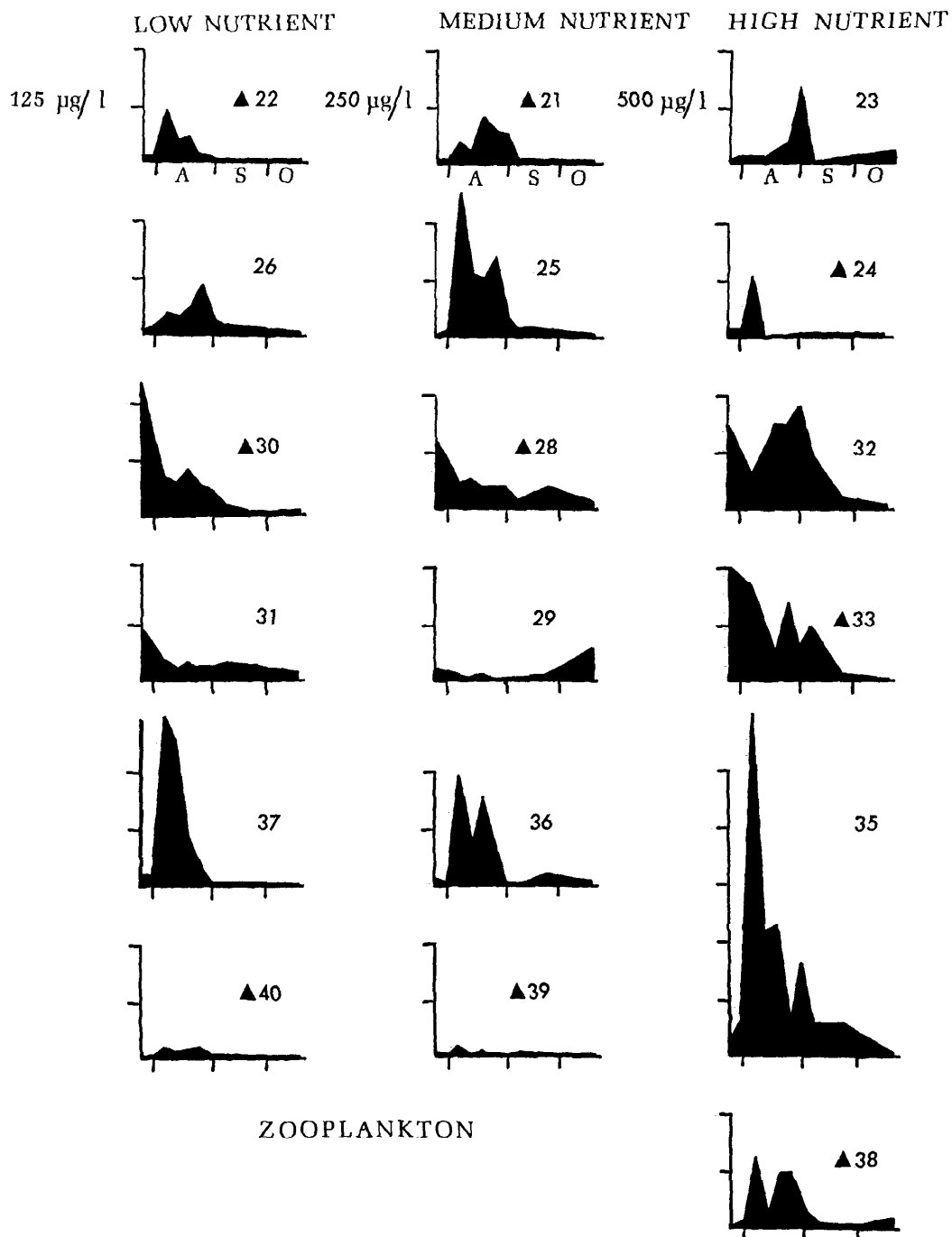
FIG. 6.   Biomass of zooplankton in 18 ponds in 1965. Different scales were used for each nutrient level.   Triangles indicate HP ponds.
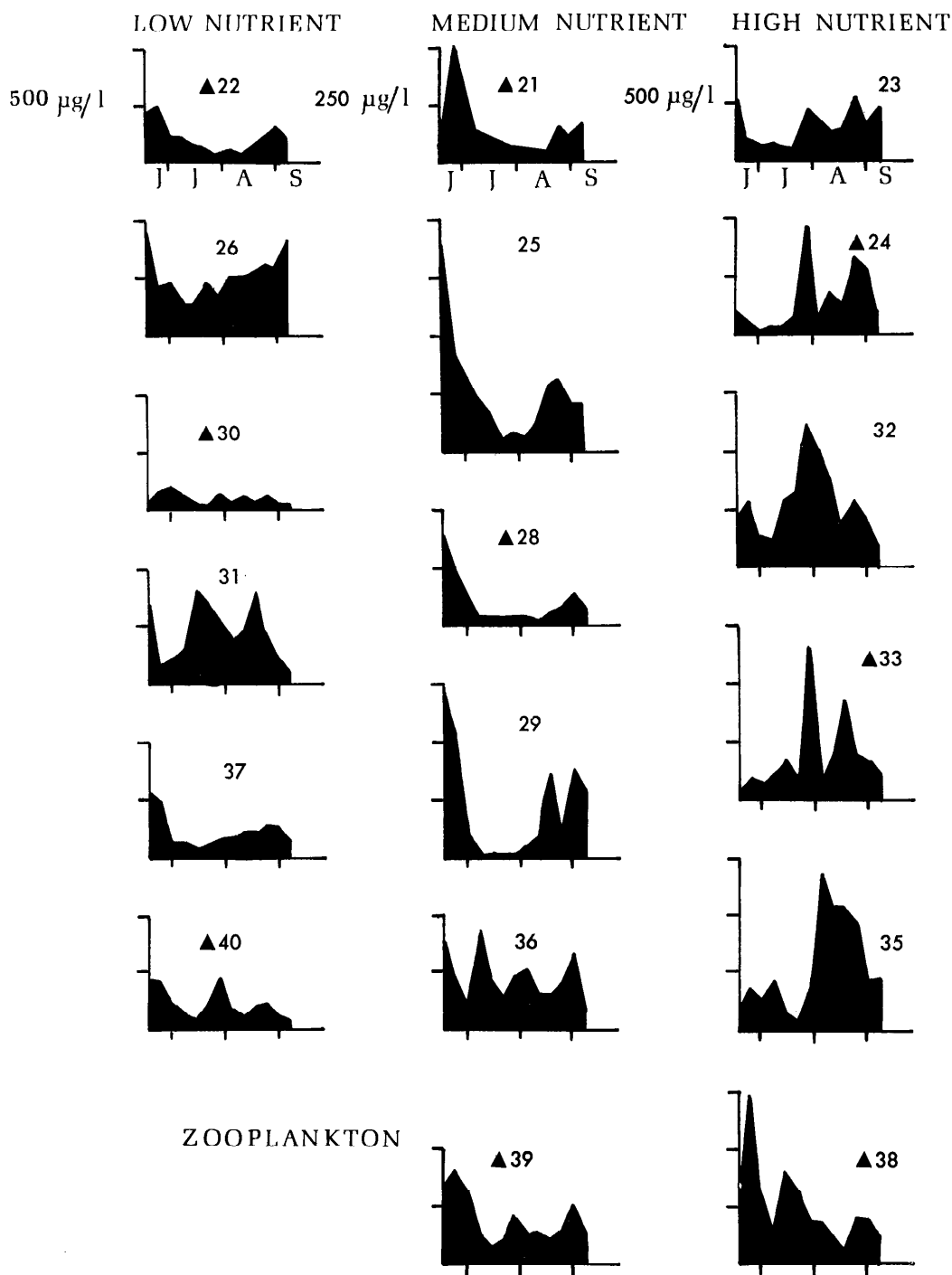
FIG. 7. Biomass of zooplankton in 18 ponds in 1966. Different scales were used for the nutrient levels. Triangles indicate HP ponds.
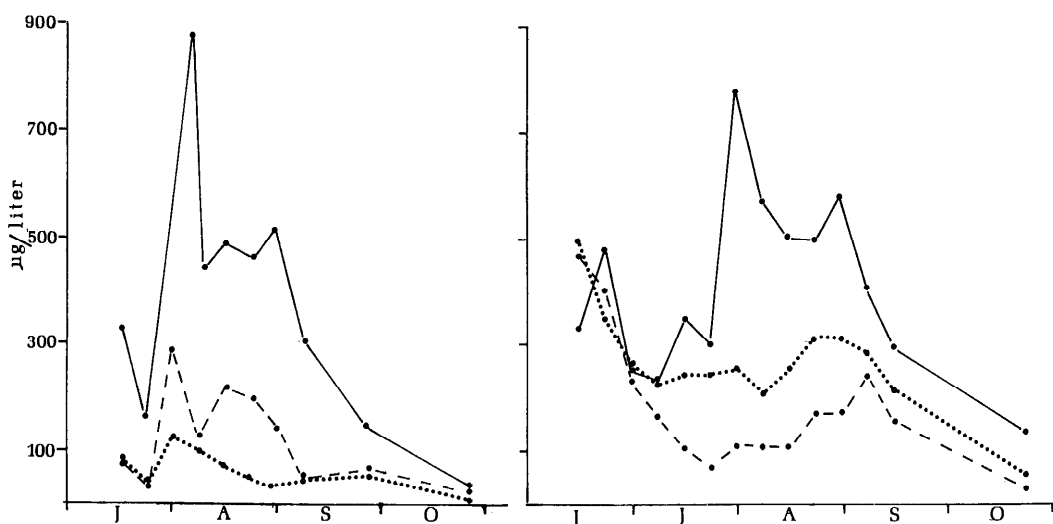
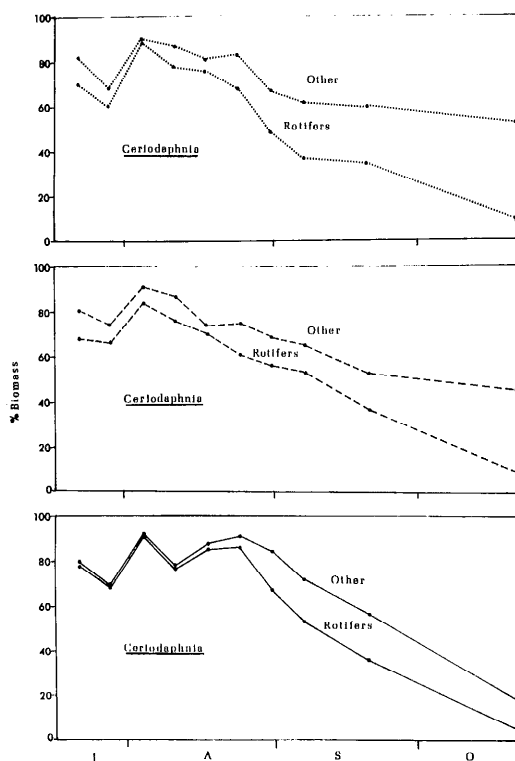FIG. 8. Mean zooplankton biomass at three nutrient levels in 1965 and 1966 (HN ———, MN – – –, LN · · ·).

FIG. 9. Mean percent species composition of zooplankton biomass at three nutrient levels in 1965 (HN ———, MN – – –, LN · · ·).

biomass (Fig. 10). *Daphnia pulex* was important in early spring but declined rapidly in June. Its disappearance was preceded by the production of large numbers of ephippia (*see* Stross and Hill 1965). The incidence of *Simocephalus serrulatus* at HN levels in 1966 coincides with the appearance of vascular plants. Combinations of these three cladocerans accounted for about 80% of the biomass from June until September at all nutrient levels. Rotifers contributed from 1–16% during summer months. Both numbers and biomass of the rotifers were dominated again by *K. cochlearis* and *Polyarthra* sp., which together constituted $73 \pm 3\%$ of the total rotifers averaged over all ponds.

Population responses. *Ceriodaphnia* instars are morphologically indistinguishable; their size differences are small and time consuming to measure. Consequently, we counted only three major life-history stages: egg, juvenile, and adult. The criterion used to distinguish juvenile from adult was the mean minimum carapace length of egg-bearing individuals (450μ in all ponds). For the numerical analysis juveniles and adults were lumped since their temporal responses were identical, although juveniles

were always more abundant. The trend of mean densities (Fig. 11) reflects a strong nutrient effect at IIN. The mean densities at HN, based on 6 ponds, tend to obscure the violent fluctuations in individual units. For the latter half of summer 1965, where adequate data are available, the mean response curves indicate a peak in August followed by a continuous decline through October. The IIN response in 1966 followed the same pattern. During June 1966, the mean *Ceriodaphnia* density was lowest in the IIN ponds, coinciding with the presence of *Daphnia*, most abundant in the HN ponds (Fig. 10). At LN and MN levels *Ceriodaphnia* densities remained relatively uniform. Egg ratios (number of eggs/female) responded similarly.

Keratella cochlearis populations were definitely depressed at HN levels (Fig. 12) in both years. *Ceriodaphnia* and *Keratella* densities were negatively related. However, *Polyarthra* did not show any depression at HN conditions (Fig. 13).

Predation

Mean zooplankton biomass was consistently higher in LP than in IIP ponds after mid-July in both years, and the magnitude of the difference was also similar (Fig. 14).

Changes in the percent composition of the community biomass suggest size-selective invertebrate predation. For 1966, the mean percent biomass of major species in LP ponds was subtracted from that in HP ponds (Fig. 15). The trends for *Ceriodaphnia*, *Daphnia*, and total rotifers show interesting relationships. In June, *Daphnia* was least abundant and *Ceriodaphnia* most abundant in high predator ponds. After *Daphnia* disappeared in early July, *Ceriodaphnia* became least abundant in high predator ponds (7 out of 9 dates), but rotifers increased in direct proportion to the decline of *Ceriodaphnia*. These trends are suggestive of direct predation first on the larger *Daphnia*, then on *Ceriodaphnia*, with the attendant increase of a smaller organism in both cases.

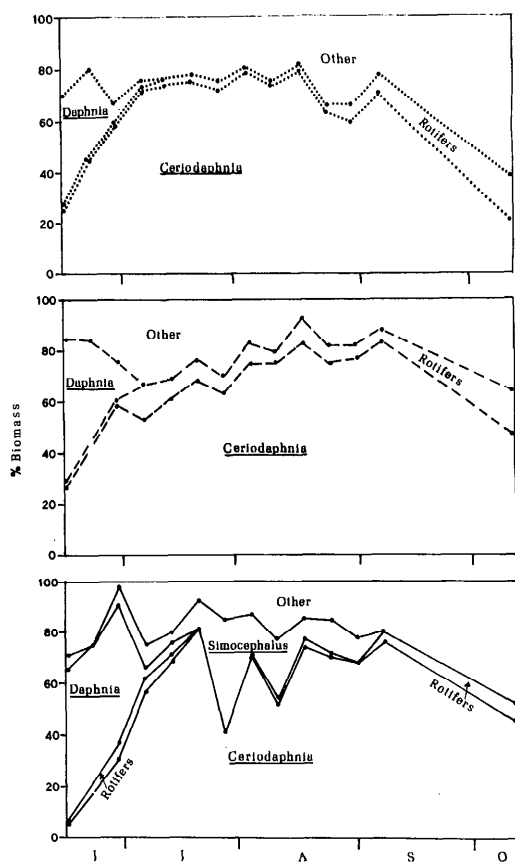The effect of predator densities on numbers of *Ceriodaphnia* is illustrated in Fig.

FIG. 10. Mean percent species composition of zooplankton biomass at three nutrient levels in 1966 (HN ——, MN — — —, LN · · ·).

16. After midsummer, both adult and juvenile stages were lower in the high predator ponds. The biomass response was essentially identical with the numerical, as would be expected when the stages studied do not greatly differ in weight or change in proportions.

The numerical response of *Keratella* to predator densities (Fig. 17) supports the observations of increased percent rotifer biomass at HP levels in late summer (Fig. 15). *Polyarthra* did not respond to predator manipulations.

Interaction of nutrients and predation

The effect of predation on *Ceriodaphnia* biomass at different nutrient levels is shown in Fig. 18. Predation apparently
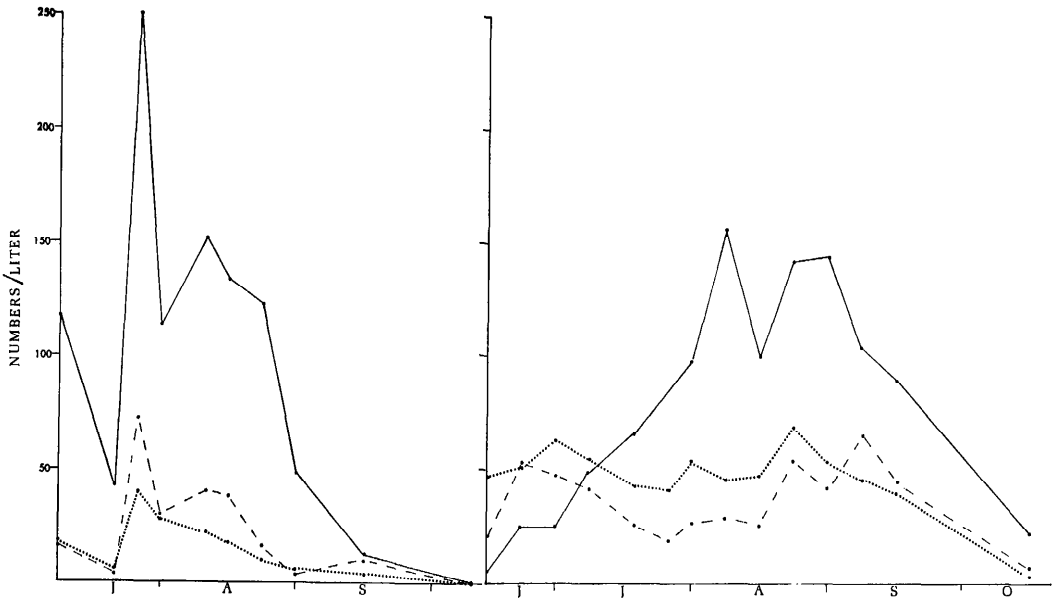
FIG. 11. Mean densities of *Ceriodaphnia* at three nutrient levels in 1965 and 1966 (HN ——, MN
– – –, LN · · ·).

exerted the same relative effect at each
nutrient level, since the points are not dis-
tributed according to nutrient level. In
1966, the seasonal trend from positive to
negative values appears related to the dis-
appearance of the *Daphnia.* On the basis
of percent numerical difference the rotifer
Keratella also failed to show any interac-
tion of nutrients and predation, although

its seasonal trend was the reverse of
Ceriodaphnia.

Production

Neither the analysis of *Ceriodaphnia* re-
sponses in terms of numerical or biomass
standing crop nor the inspection of popu-
lation trends, size distributions, or brood
sizes in field populations is sufficient to
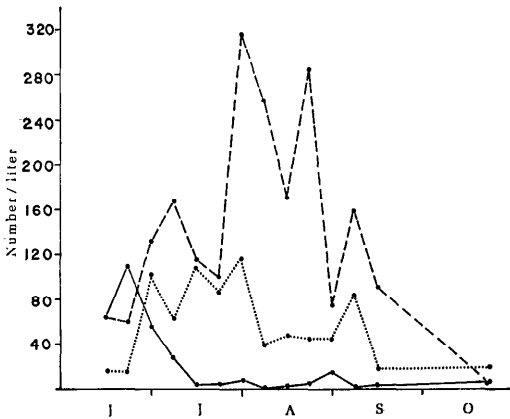
FIG. 12. Mean numerical densities of *Keratella
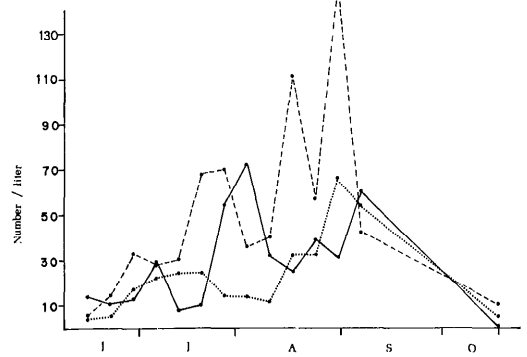cochlearis* at three nutrient levels in 1966 (HN
——, MN – – –, LN · · ·).

FIG. 13. Mean numerical densities of *Poly-
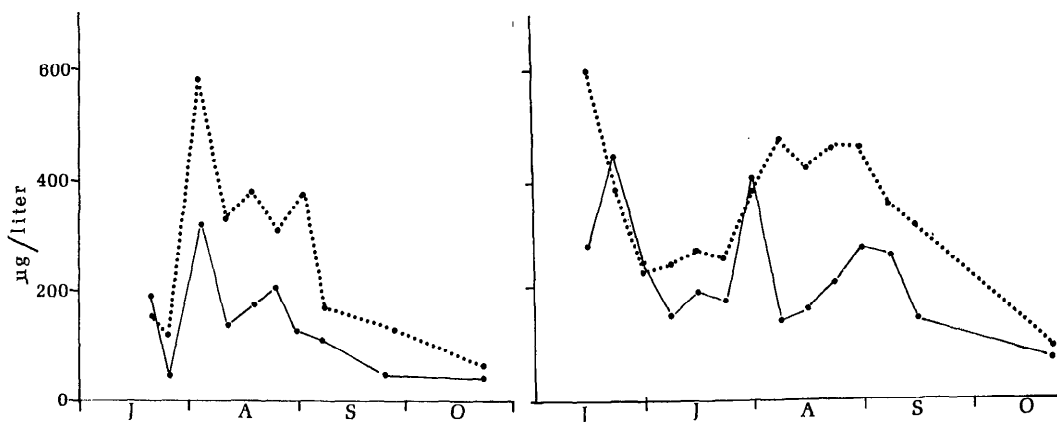arthra* at three nutrient levels in 1966 (HN ——,
MN – – –, LN · · ·).

FIG. 14.   Mean zooplankton biomass at two predation levels in 1965 and 1966 (HP ——, LP · · ·).

permit the estimation of growth or turnover rates. Laboratory or field experiments are necessary for the measurement of critical rate functions.

Two types of life table experiments were performed on *Ceriodaphnia*. One was done in the laboratory under constant light at 23C. Newborn *Ceriodaphnia* were grown individually in 175-cc glasses containing 120 cc of medium. A mixture of *Scenedesmus*, *Ankistrodesmus*, and *Chlorella*, grown in aerated carboys (19 liters) on Bristol's medium with soil extract, served as the food source. Two cohorts of 10 *Ceriodaphnia* each were raised at a food level of 4 Klett OD units (about 4×10^5 cells/cc); another cohort of 10 was raised at 0.5 Klett units. The medium was changed daily and each animal observed to determine maturation time (from hatching to the release of the first young), developmental rate of eggs, duration of adult instar, brood size, and median survival time.

Three life table experiments were performed in the field—one each at HN, MN, and LN. Ten newborn *Ceriodaphnia* were placed in a 140-cc jar (= 70 animals/liter). Five closed jars were fixed at equal distances along a 1.2-m plank anchored vertically in the pond, so that cohorts were exposed to the conditions at different depths. Each day the apparatus was removed from the pond and taken to a nearby laboratory where the jars were examined

for survivors, eggs, and young. Young were discarded. Each cohort was then transferred with a medicine dropper to a clean jar containing unfiltered water from the appropriate pond. The entire process took 1 or 2 hr. In addition, individual newborn *Ceriodaphnia* were placed in jars and examined according to the above technique, to secure more precise estimates of rate functions.

No previous comparisons have been reported between laboratory and field life tables for zooplankton. The results from the laboratory and field are similar, except for the low food maturation time in the laboratory (Table 8). The two experiments yield the same rate functions, even though
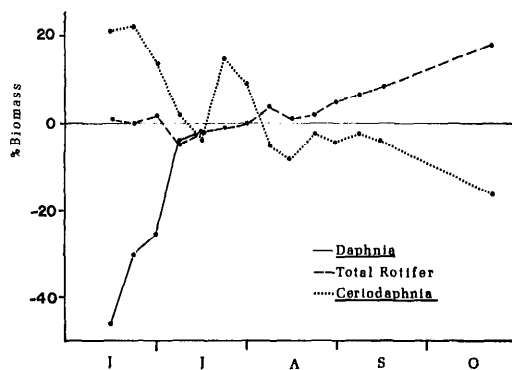

FIG. 15.   Differences in mean percent biomass contribution of three zooplankters expressed as HP minus LP in 1966.
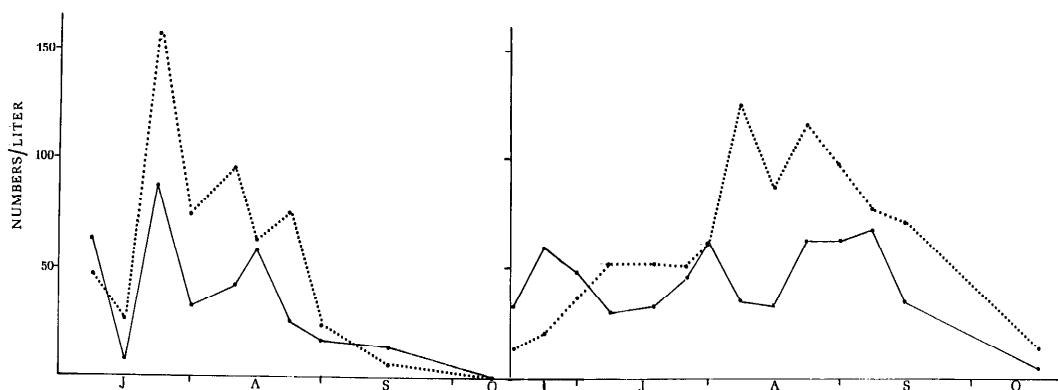
FIG. 16.   Mean densities of *Ceriodaphnia* at two predation levels in 1965 and 1966 (HP ——, LP · · ·).

temperatures in the field fluctuated from 20 to 26C and the laboratory remained a constant 23C. The rates of maturation and egg development seem unaffected by different nutrient levels in the ponds. A maturation time of 3.5 days and egg development time of 2.0 days have been chosen as the best estimates. Median survival was between 2 and 3 weeks.

Instantaneous rates of increase (Table 9) were calculated from laboratory and field life table data according to Andrewartha and Birch (1954). Under near optimal laboratory conditions, *Ceriodaphnia* exhibits an instantaneous rate of increase (r) of 0.58. The mean r value from the ponds (Table 10) indicates a rapid population turnover.

At summer temperatures, *Ceriodaphnia* has a mean generation time of about 7 days ($T = \ln R_o/r$). The large fluctuations in

Figs. 6 and 7 are apparently due to changing egg densities and mortality rates, since maturation and egg development rates are relatively constant.

Life table experiments with S. *serrulatus* were also performed as described above in both laboratory and ponds. The laboratory experiment consisted of 10 individuals in an algal medium of 8 Klett units. At this high food level, mean maximum brood size (31 ± 1.8 eggs) and the calculated instantaneous rate of increase ($r = 0.55$) were both large. The field experiments yielded an r value of 0.27 ± 0.033, but the duration of egg development (2.0 days), maturation time (6.5 days), and median survival (about
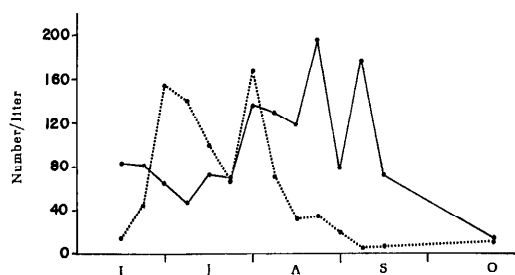

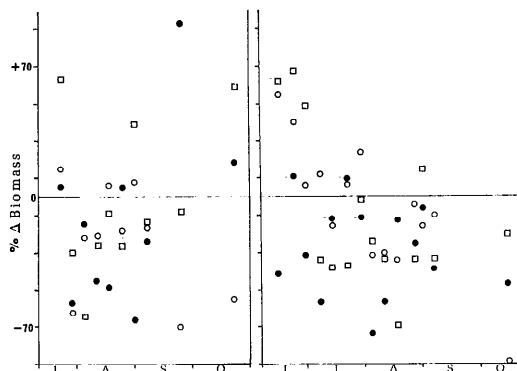FIG. 17.   Mean numerical densities of *Keratella cochlearis* at two predation levels in 1966 (HP ——, LP · · ·).

FIG. 18.   Mean percent difference of *Ceriodaphnia* biomass between HP and LP ponds expressed as [(HP − LP)/(HP + LP)] × 100 at three nutrient levels in 1965 and 1966 (HIN = ●, MN = □, LN = ○).

TABLE 8. *Rate function estimates of* Ceriodaphnia

	Median days	n
I. Laboratory life tables at 23C		
A. Maturation times (mean days $\pm$ SE)		
4 Klett 3.0 $\pm$ 0.11	3.5	28
0.5 Klett 5.0 $\pm$ 0.50	4.5	6
B. Egg development time (mean days $\pm$ SE)		
4 Klett 1.8 $\pm$ 0.04	1.8	38
0.5 Klett 1.8 $\pm$ 0.09	1.8	18
II. Field life tables* at mean temperatures of 23C		
A. Maturation time		
HN 3.8 $\pm$ 0.14	3.5	11
MN 3.2 $\pm$ 0.17	3.5	9
LN 3.1 $\pm$ 0.24	3.5	5
B. Egg development time		
HN 1.9 $\pm$ 0.08	2	10
MN 1.8 $\pm$ 0.11	1.8	6
LN 1.9 $\pm$ 0.12	2	4

* Plus numerous estimates using cohorts of 10 from which modal values of egg development times were determined.

TABLE 9. *Life table of* Ceriodaphnia. *Food level* $= 4$ *Klett units; temperature* $= 23C \pm 1°$

Pivotal age	l_x	m_x	$l_x m_x$	
0	1.0	0	—	estimated T
0.5	1.0	0	—	$= 812.90/78.15$
1.5	1.0	0	—	$= 10.4$ days
2.5	1.0	0	—	estimated r
3.5	1.0	3.6	3.6	$= (\ln R_0)/T$
4.5	1.0	0	0	$= 0.42$
5.5	0.9	7.7	6.93	$l_x m_x e^{-rx} = 1.00$
6.5	0.9	5.0	4.50	(solve for r by trial
7.5	0.8	3.3	2.64	and error substi-
8.5	0.8	9.7	7.76	tution)
9.5	0.8	1.7	1.36	$r = 0.58$
10.5	0.8	8.2	6.56	$T = 7.5$ days
11.5	0.8	9.6	7.68	
12.5	0.8	1.6	1.28	
13.5	0.8	8.2	6.56	
14.5	0.8	10.2	8.16	
15.5	0.7	4.7	3.29	
16.5	0.7	6.8	4.76	
17.5	0.7	8.8	6.16	
18.5	0.7	1.3	0.91	

$78.15 = R_0 =$ net reproductive rate

20 days) agreed with the laboratory experiment. Mean generation time (T) was 10 days.

Life table experiments were also run in the laboratory on the rotifers *K. cochlearis*, *Filinia* sp., *Polyarthra* sp., *Keratella hiemalis*, *Platyias patulus*, and *Syncheata pectinata*. It was difficult to obtain rate functions because none of these species cultures easily. Individual rotifers were collected and put in a depression slide containing 0.4 cc of pond water which was changed semidaily. Two strategies were used following Edmondson (1960). The first was to begin with nonegg-bearing females and, by frequent observation, determine to the nearest 1 or 2 hr when an egg was produced, and then determine the time for it to hatch. This yields the duration of egg development directly and can be considered an accurate estimate if natural food and ambient temperatures are maintained and if observations are frequent. The second approach was to select only egg-bearing females and determine the time until hatching. This method assumes that eggs are produced continuously and that any randomly selected group of females contains equal numbers of eggs at each stage of development. By determining the average time to hatching for all eggs and then doubling this, a rough estimate of egg developmental time is obtained.

All but one of the above estimates for several species of rotifer eggs were ≤ 24 hr. These results agree with those of Edmondson (1960) for development times at different temperatures for the eggs of several rotifers, including *K. cochlearis*. Because of difficulties in culturing, we could not determine the period of maturation and median survival time. Kolisko (1938) determined the maturation time (4 days) and average adult lifespan (18 days) for *Keratella valga* at 17C. If her estimates are converted to 23C, according to the curves in Edmondson (1960), we get an estimated maturation time of 1.5 days and a median lifespan of about 6 days. Others (Edmondson 1946, 1960; King 1967) have reported nearly iden-

TABLE 10. *Replicated field life table estimates of the instantaneous rate of increase* (r) *and mean generation time* (T) *in days for* Ceriodaphnia

Pond No. 24, high nutrient	
$r_1 = 0.35$	$T_1 = 7.7$
$r_2 = 0.43$	$T_2 = 7.7$
$r_3 = 0.37$	$T_3 = 6.9$
$r_4 = 0.28$	$T_4 = 8.6$
$r_5 = 0.31$	$T_5 = 9.6$
$r_{\bar{x}} = 0.35$	$T_{\bar{x}} = 8.1$

Pond No. 25, medium nutrient	
$r_1 = 0.43$	$T_1 = 6.7$
$r_2 = 0.41$	$T_2 = 6.2$
$r_3 = 0.49$	$T_3 = 5.5$
$r_4 = 0.40$	$T_4 = 7.6$
$r_5 = 0.47$	$T_5 = 7.3$
$r_{\bar{x}} = 0.44$	$T_{\bar{x}} = 6.7$

Pond No. 26, low nutrient	
$r_1 = 0.60$	$T_1 = 7.1$
$r_2 = 0.58$	$T_2 = 6.3$
$r_3 = 0.58$	$T_3 = 6.3$
$r_4 = 0.34$	$T_4 = 7.2$
$r_5 = 0.48$	$T_5 = 6.5$
$r_{\bar{x}} = 0.52$	$T_{\bar{x}} = 6.7$

Grand mean $= 0.44 \pm 0.024$	Grand mean $= 7.2 \pm 0.26$

tical values for different rotifers at similar temperatures.

King (1967) has found egg development rates, maturation time, and instantaneous rates of increase (r) under controlled laboratory conditions for the littoral rotifer, *Euchlanis dilatata*. These values are slightly higher than those of most planktonic rotifers at normal temperatures. King's single highest value of r, based on optimal laboratory growth conditions at 22C, gives a potential turnover rate some 2.3 times greater than *Ceriodaphnia*: [rotifer (r_{max})]/[*Ceriodaphnia* (r_{max})] = 1.4/0.6 = 2.3. If instead, we select King's high mean value of r (0.76), then the ratio of rotifer turnover rates to *Ceriodaphnia* drops to 1.3. In either case, the percent biomass data in Figs. 9 and 10 reveal that rotifers, on the basis of greater turnover, could not dominate *production* until very late in the season (September–October), at which time the standing crop is greatly reduced and rates have decreased because of falling temperatures.

An r of 0.76 will allow a rotifer popula-tion turnover once per day or 7-fold in a week. Since sustained optimal conditions in the ponds throughout summer are unlikely, a 3-fold turnover each week appears to be more realistic. This is similar to the highest rotifer turnover rates estimated by Hillbricht-Ilkowska (unpublished).

The above data permit us to calculate the production of the dominant populations. A realistic production model must include rates of recruitment, growth, and mortality. Two types of mathematical models are commonly used for this purpose. For species with nonoverlapping generations (e.g., many insects), a discrete growth equation is used in which morphological or physiological life-history stages serve as the categories through which the population passes. In each of these categories a different set of individual growth and mortality factors operates. Production is then, by extrapolation, simply a summation across the generation time or any desired part of it. The other type of model is based on the instantaneous growth equation and is most frequently used for organisms with short, overlapping generations (bacteria, algae, and zooplankton).

Ceriodaphnia would seem to fit in the latter category, but there is no *a priori* reason why production could not be adequately estimated with a set of iterative, discrete growth equations. The production *interval*, however, must be short enough to avoid a ponderous expression. Our sampling interval was usually 7 days, so we generated a numerical model to operate over this time span.

Our model is based on the following set of unreduced equations:

$$A_t = s_2 A_0 + \frac{J_0}{a} a s_1 s_2 + \frac{E_0}{b}(t-a) s_1 s_2^2$$
$$+ J_0 \frac{E_0/b}{A_0}(t-a) s_1^2 s_2^2; \qquad (1)$$

$$J_t = \frac{E_0}{b} a s_1 s_2 + \frac{J_0}{a} a \frac{E_0/b}{A_0} \frac{a}{t} t s_1^2 s_2$$
$$+ \frac{E_0}{b}(t-a) \frac{E_0/b}{A_0} a s_1^2 s_2^2; \qquad (2)$$

$$E_t = E_0 s_2 + J_0 \frac{E_0}{A_0} s_1 s_2 + \frac{E_0}{b}(t-a)\frac{E_0}{A_0} s_1 s_2{}^2$$

$$+ J_0 \frac{E_0/b}{A_0}(t-a)\frac{E_0}{A_0} s_1{}^2 s_2{}^2; \qquad (3)$$

A_t = predicted number of adults at t,
A_0 = initial number of adults;
J_t = predicted number of juveniles at t,
J_0 = initial number of juveniles;
E_t = producted number of eggs at t,
E_0 = initial number of eggs;
t = time interval;
a = maturation time (hatching to first young) = 3.5 days;
b = egg development time = 2.0 days;
s_1 = survival of juveniles = 0.9;
s_2 = survival of adults = 0.7.

An example will illustrate the use of the model. Suppose 100 adult *Ceriodaphnia* were present initially. Their age distribution is unknown. We apply a fixed survivorship (*not* survival rate) of 70% to the weekly time interval or any part thereof which yields 70 adults. (Note that adults in Table 9 had 70% survivorship even after 2 weeks.) Eventually, the remaining adults will die rather quickly according to a rectangular survival curve; this aspect was not included in the model. An initial 100 juveniles experience a fixed survivorship of 90% and, when adults are reduced further by 30%, yield 63 adults. An initial 100 eggs are divided by their development time to give eggs hatching per day, which are multiplied by the number of days in the sampling interval exceeding the maturation period $(t-a)$. This operation eliminates the new individuals still present as juveniles at the end of the interval. If $t = 7$, then the result is 175 individuals times both survivorship constants, or 100 adults. From the last term in equation (1) we calculate the adults produced from the eggs of initial juveniles; assuming an egg ratio identical with the initial ratio, $E_0 : A_0$, we get 70 more adults. Summing, we have a predicted 313 adults after 1 week. The calculation of juveniles follows the same reasoning. We have somewhat arbitrarily applied survivorship constants. A more ele-

gant and possibly more accurate method would have been to assume a constant survival *rate* in each age category and raise this rate to the t power ($s_1{}^t$ and $s_2{}^t$). However, we used our method because of the nature of the survivorship data and for comparative use of the production model.

Predicted numbers of adults and juveniles were multiplied by their individual mean dry weights and the two categories combined to yield an estimate of *Ceriodaphnia* biomass at t. The initial biomass (less the intrinsic mortality on adults and juveniles during the interval) has been subtracted from this predicted biomass, yielding the production estimate. Negative production values, of course, indicate a larger initial biomass than that estimated 1 week later; these rarely occurred. The weekly production estimates for each pond were then added, yielding the seasonal response of *Ceriodaphnia* to the experimental manipulations.

Total rotifer production was estimated by multiplying the weekly rotifer biomass estimate in each pond by the constant turnover factor of 3, and then summing for the summer.

The total production estimates combine *Ceriodaphnia*, rotifer, and *Simocephalus* production. This translates more than 75% of the standing biomass into production estimates. Tables 11 and 12 reveal that increased nutrient levels augmented total production in 1965 (significant at 0.05 level) but not in 1966. Increased predation had no significant effect on production at any nutrient level. *Ceriodaphnia* dominated the production response in both years (95 and 85% respectively). Total rotifer production appears to be positively related to both nutrient and predation levels in both years, with a predation effect evident at each nutrient level. Unlike that of *Ceriodaphnia*, rotifer production increased at HP. In both years rotifer production was less than 10% of the total. *Simocephalus* was nearly absent in 1965, but it contributed 10% of the production of each pond in 1966.

Comparison of production estimates for the 2 years (Table 13) is difficult because

TABLE 11. *Zooplankton production estimates ($\overline{X} \pm$ SE) expressed as µg/liter dry wt for summer 1965 and percent contribution of dominant species*

	Total production	Ceriodaphnia (%)	Rotifers (%)
HN	5,762 ± 1,750	5,606 ± 1,731 (97)	156 ± 40 (3)
MN	1,316 ± 338	1,244 ± 345 (95)	72 ± 15 (5)
LN	963 ± 179	905 ± 185 (94)	58 ± 16 (6)
HP	2,331 ± 1,110	2,206 ± 1,088 (95)	125 ± 27 (5)
LP	3,029 ± 1,126	2,964 ± 1,113 (98)	65 ± 20 (2)
HNHP	4,858 ± 3,079	4,655 ± 3,027 (96)	203 ± 52 (4)
HNLP	6,666 ± 2,241	6,557 ± 2,215 (98)	109 ± 55 (2)
MNHP	1,274 ± 587	1,187 ± 602 (93)	87 ± 29 (7)
MNLP	1,356 ± 474	1,300 ± 480 (96)	56 ± 6 (4)
LNHP	860 ± 346	776 ± 354 (90)	84 ± 23 (10)
LNLP	1,066 ± 173	1,035 ± 173 (97)	31 ± 1 (3)

of the different periods over which production was calculated (8 and 12 weeks). Most of the production in the HN ponds in 1966 occurred during the last 8 weeks of summer; thus at HN levels production estimates for 1965 and 1966 are comparable and similar. At LN and MN levels, however, much of the production occurs earlier in the summer so that the 1965 values may be considerably underestimated.

Summary

Total zooplankton biomass reached the greatest densities at HN levels in both years. The magnitude of the response was nearly identical. At MN levels the response was inconsistent; standing crop was somewhat higher than the LN levels in 1965, but definitely lower in 1966. The community was dominated at all three nutrient levels by *Ceriodaphnia*. This species responded to the experimental manipulations in similar fashion in both years. Rotifers also showed a consistent response in 1965 and 1966. In both years, over 70% of the sampling dates revealed an average 2-fold difference in mean biomass due to invertebrate predation. This effect was maintained at all three nutrient levels. The predator pressure on *Ceriodaphnia* populations essentially generated the above pattern, while rotifers exhibited the reverse,

TABLE 12. *Zooplankton production estimates ($\overline{X} \pm$ SE) expressed as µg/liter dry wt for summer 1966 and percent contribution of dominant species*

	Total production	Ceriodaphnia (%)	Rotifers (%)	Simocephalus (%)
HN	4,756 ± 647	3,908 ± 525 (82)	349 ± 79 (7)	499 ± 251 (10)
MN	3,514 ± 578	2,972 ± 466 (85)	268 ± 83 (8)	274 ± 57 (8)
LN	3,925 ± 405	3,322 ± 427 (85)	146 ± 34 (4)	457 ± 60 (12)
HP	3,911 ± 343	3,283 ± 286 (84)	288 ± 67 (7)	340 ± 58 (9)
LP	4,218 ± 554	3,518 ± 483 (83)	220 ± 54 (5)	480 ± 164 (11)
HNHP	4,415 ± 680	3,658 ± 431 (83)	391 ± 114 (9)	366 ± 180 (8)
HNLP	5,097 ± 1,250	4,158 ± 1,062 (82)	306 ± 129 (6)	633 ± 514 (12)
MNHP	3,440 ± 462	2,857 ± 357 (83)	309 ± 154 (9)	274 ± 25 (8)
MNLP	3,586 ± 1,197	3,086 ± 961 (86)	227 ± 95 (6)	273 ± 126 (8)
LNHP	3,878 ± 705	3,334 ± 693 (86)	164 ± 61 (4)	380 ± 60 (10)
LNLP	3,970 ± 561	3,310 ± 657 (83)	127 ± 44 (3)	533 ± 92 (13)

positive response in HP ponds. Production estimates show similar trends. There was no indication of an interaction of nutrients and predation in the zooplankton data.

Methods 1967

Dense stands of *Elodea* (ponds 23 and 24), clumps of filamentous algae (pond 35), and blooms of *Microcystis* (ponds 32 and 33) forced us to use two new sampling methods in the HN ponds in 1967. Beginning 12 July, two vertical net hauls (90 liters of water each), were taken instead of the normal sampling procedure in ponds 32 and 33. The No. 20 net became clogged with *Microcystis* if larger volumes were sampled. Beginning on 3 August, samples from ponds 23, 24, and 35 were collected with a 0.5-liter widemouth jar attached to a pole. When the rubber stopper was jerked out, the jar filled so forcefully that weed-dwelling crustaceans were swept in. Two sets of 6-jar samples were collected from each of these ponds at 0.1 and 0.5 m; each replicate represents 3 liters of pond water. The samples were concentrated with a No. 20 net. The dip-jar sampler was compared to the net tows on one occasion and, although it varied with the species counted, the net was about 50% as efficient as the jar. A 2-fold correction for sampling efficiency is made when zooplankton production estimates are combined or compared with benthos production.

Results 1967

Nutrients

Total biomass. Total biomass for individual ponds is given in Fig. 19. The LN and MN ponds had maximal values in June, although as in previous years, HN ponds reached their peak in July or August. The seasonal trends in total biomass are given in Fig. 20. The LN and MN ponds reached a peak (500–600 μg/liter) in mid-June and then returned to previous levels (about 150 μg/liter). HN ponds changed little from May to July (<300 μg/liter). A gradual increase in July preceded the sudden maximum in August (>1,800 μg/liter),

TABLE 13. *Mean summer total biomass (μg/liter) and production of zooplankton*

Nutrient level	Biomass			Production		
	1965*	1966	1967	1965*	1966	1967
LN	67	259	124	963	3,925	3,412
MN	104	141	134	1,316	3,514	3,034
HN	416	492	1,734	5,762	4,756	11,823
$\overline{X}$/pond	196	297	664	2,680	4,065	6,990

* Based on last 8 weeks only; 1966 and 1967 included 12-week period from 15 June–7 September.

but by early September, total biomass declined again (<600 μg/liter).

Community composition. The zooplankton community was much more complex in 1967 than in previous years, but fish predation exerts an overwhelming effect on species composition so an analysis based on nutrient effect alone would be misleading. The results are included in the predation and interaction sections below.

Population responses. Dominance in the zooplankton community was shared by more species than during the previous 2 years. *Ceriodaphnia* showed the same response to nutrient levels as in 1966 (Fig. 21). Populations in HN ponds exhibited low densities until mid-July, increased in early August to peaks of >50 adults/liter and >100 juveniles/liter, and then rapidly declined by 7 September. Following an initial pulse in mid-June, *Ceriodaphnia* at LN and MN levels declined to near constant densities for the rest of the summer. Egg densities followed those of adults; juveniles were always about twice as abundant as adults.

A similar pattern was evident in *Chydorus* populations (Fig. 22). *Chydorus* showed mid-June maxima in both LN and MN ponds, but by late July had disappeared from LN ponds and appeared only sporadically in MN ponds. The populations in HN level ponds increased gradually until late July, after which a strong growth pulse occurred (>500/liter), and then declined through September.

The small cladoceran *Bosmina* was abundant only in early summer (Fig. 23). This species responded inversely to nutrient
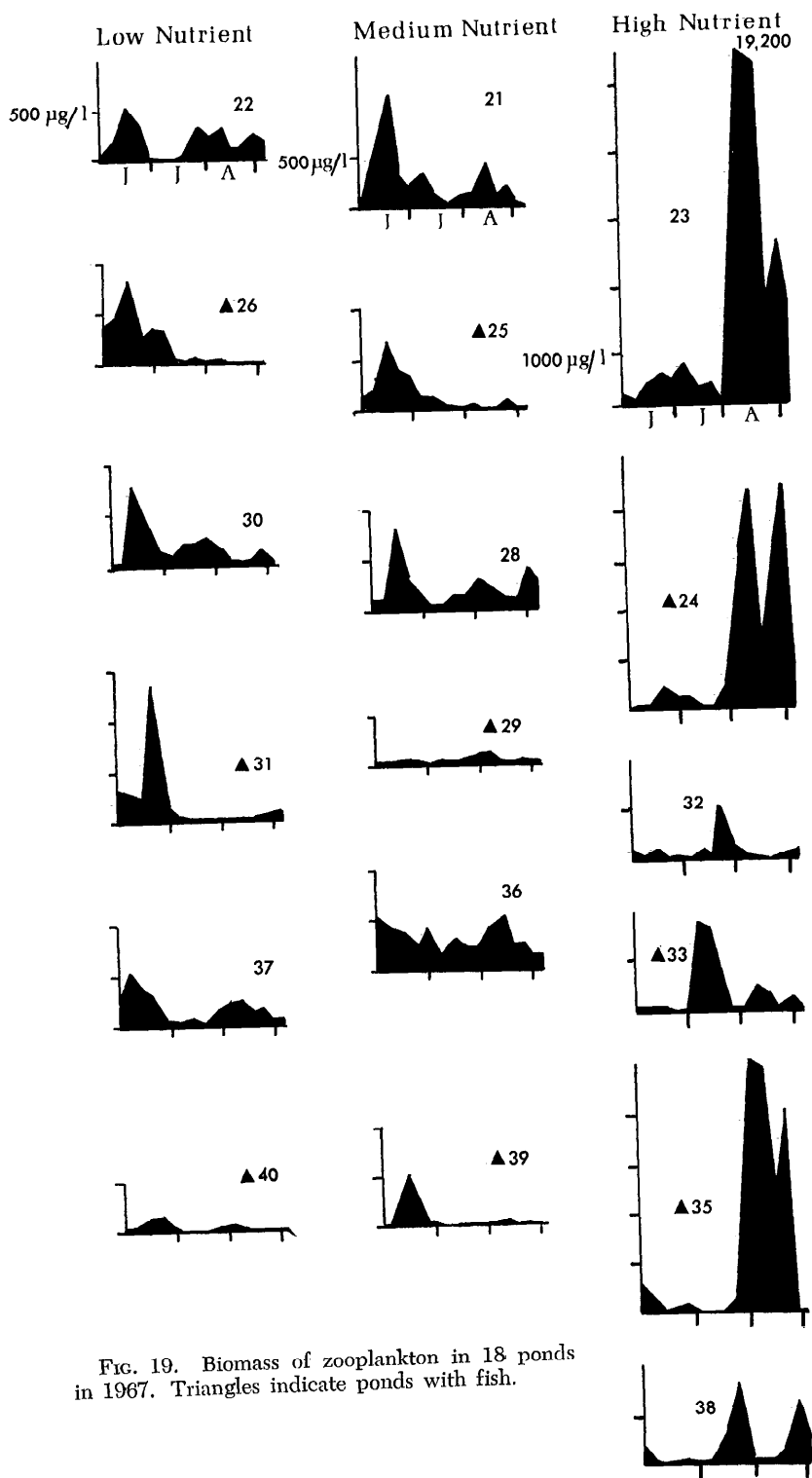
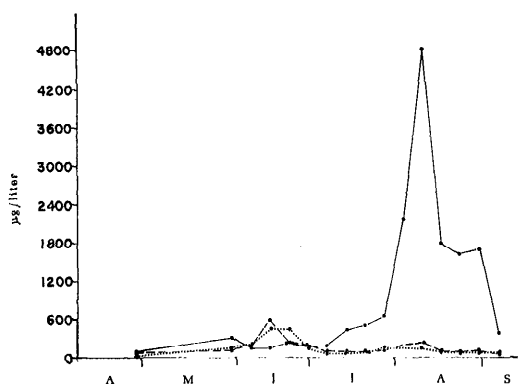FIG. 19. Biomass of zooplankton in 18 ponds in 1967. Triangles indicate ponds with fish.

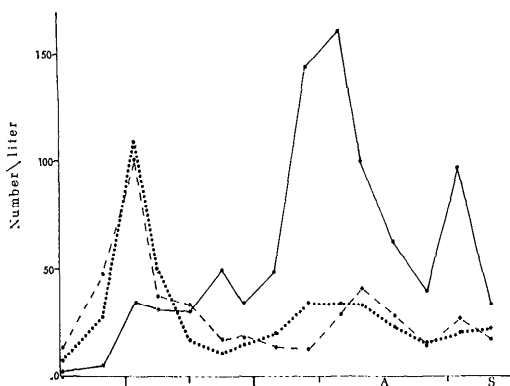FIG. 20. Mean biomass total zooplankton at three nutrient levels in 1967 (HN ——, MN – – –, LN · · ·).

FIG. 21. Mean densities of *Ceriodaphnia* at three nutrient levels in 1967 (HN ——, MN – – –, LN · · ·).

levels. Its greatest densities (>100/liter) were associated with LN levels (especially ponds 26 and 31), and it was rarely in evidence at HN levels.

In addition to being sampled as above, the weed-dwelling *Simocephalus* was also sampled by an independent, daytime survey of all ponds. This animal was rare in dip-jar samples from LN and MN ponds collected on widely spaced dates. But weekly HN samples collected in July and August revealed average densities of >100/liter and on two occasions the numbers rose to >600/liter in the weeds.

The aggregate response of rotifers shows a positive nutrient effect (Fig. 24). Highest densities were associated with HN ponds. Minimal densities at all levels occurred in June. Populations at HN levels grew rapidly during July and reached maximum densities of 2,000–6,000 animals/liter in August; rotifers in LN and MN populations rarely exceeded 400/liter.

Keratella hiemalis dominated HN ponds in 1967 with peak abundances in April–May and again in August. *Keratella cochlearis* was least abundant in HN ponds in early summer, but by August it became most abundant at HN levels, as in previous years. These two species of *Keratella* contributed 53 ± 3% of the numbers of rotifers at all nutrient levels during 1967. *Polyarthra* sp., *Filinia* sp., and *Synchaeta* were occasionally abundant. *Asplanchna* showed

no trends correlated with nutrient level. Densities reached 16, 50, and 27/liter in LN, MN, and HN ponds; median densities were about 4/liter. The dry weight of *Asplanchna* is 200 times greater than that of most other rotifers; this accounts for its relatively larger contribution to the community biomass at LN and MN levels.
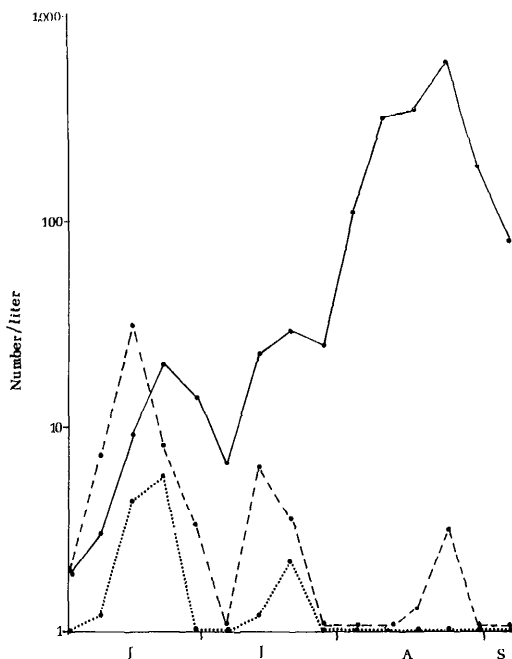

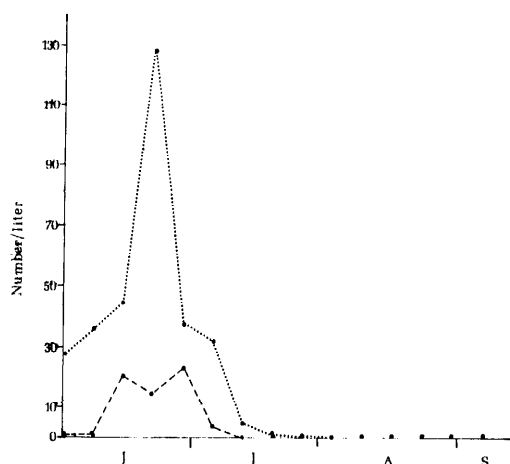FIG. 22. Mean numerical densities of *Chydorus* at three nutrient levels in 1967 (HN ——, MN – – –, LN · · ·).

FIG. 23. Mean numerical densities of *Bosmina* at three nutrient levels in 1967 (HN ——, MN – – –, LN · · ·).

Predation

Fish had no effect on total biomass of the zooplankton community but had a strong effect on community composition (Figs. 25 and 26). *Ceriodaphnia* contributed an
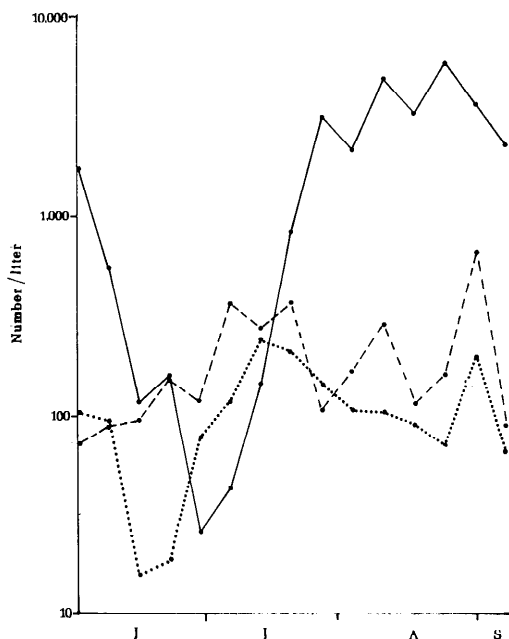

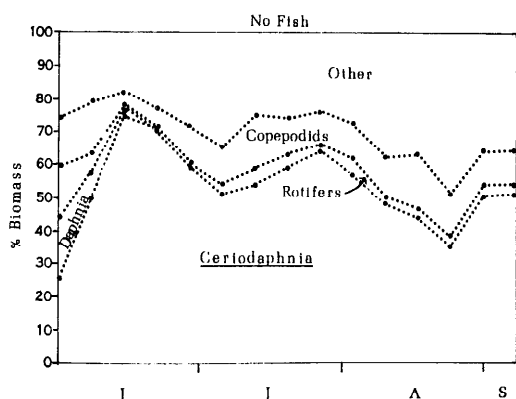FIG. 24. Mean numerical densities of rotifers at three nutrient levels in 1967 (HN ——, MN – – –, LN · · ·).

FIG. 25. Mean percent biomass contribution of dominant zooplankters in ponds with no fish in 1967.

average of 53% of the total biomass in ponds with no fish and copepodids about 10%. In ponds with fish, *Ceriodaphnia* contributed only 3% of the biomass, while *Bosmina, Simocephalus, Asplanchna, Chydorus,* copepodids, and rotifers each accounted for a sizable share of the community. Predation clearly increased species diversity.

Characteristics of the *Ceriodaphnia* populations in ponds with and without fish were strikingly different (Fig. 27). Both adults and juveniles were extremely rare (<1.0/liter) in ponds with fish for the first 9 weeks of summer, increased rapidly in early August, were near zero by 16 August, and then again increased slightly until
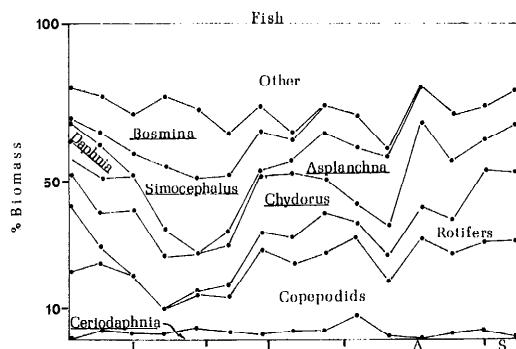

FIG. 26. Mean percent biomass contribution of dominant zooplankters in ponds with fish in 1967.
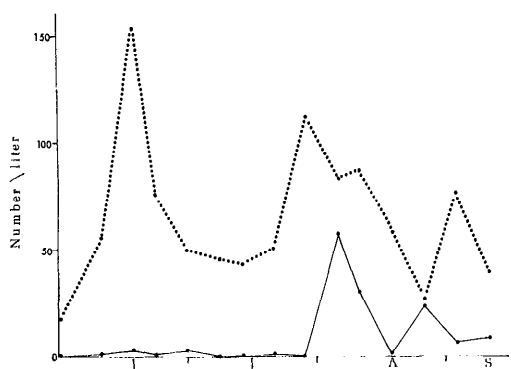
FIG. 27. Mean densities of *Ceriodaphnia* in ponds with and without fish in 1967 (F ——, WF · · ·).

FIG. 29. Mean numerical densities of *Bosmina* in ponds with and without fish in 1967 (F ——, WF · · ·).

September. In ponds without fish, *Ceriodaphnia* reached peak abundance in mid-June followed by a midsummer trough and a second peak in early August. By September the populations were much reduced.

Chydorus showed a positive response to predation (Fig. 28), and *Bosmina* occurred exclusively in ponds with fish (Fig. 29). Densities of *Simocephalus* from ponds with and without fish overlapped completely. Beginning in mid-July rotifer densities in
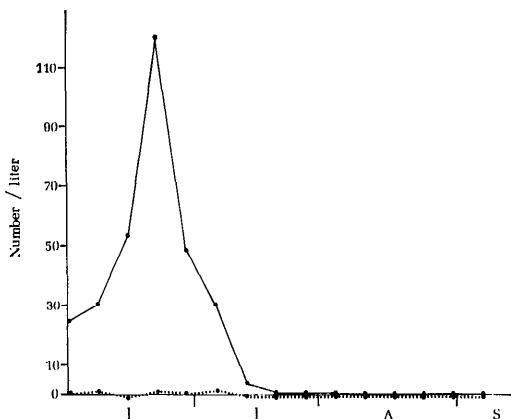
ponds with fish became 3–6 times greater than in ponds without fish (Fig. 30).

Interaction of nutrients and predation

The predation effect at specific nutrient levels (Fig. 31) shows several interesting interactions. At LN levels, total biomass was not reduced by predation until mid-July, after which the values were much smaller in ponds with fish. At MN levels,
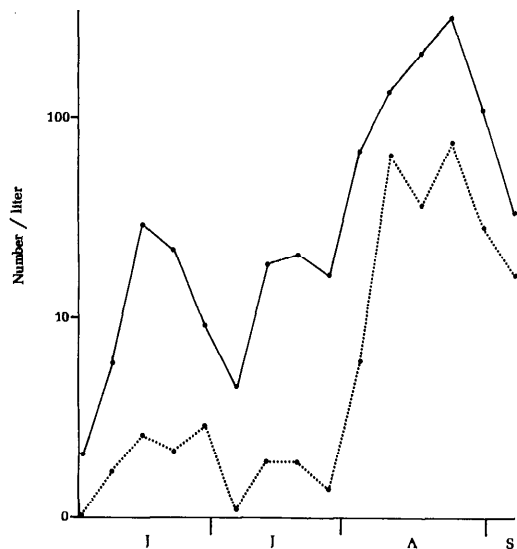

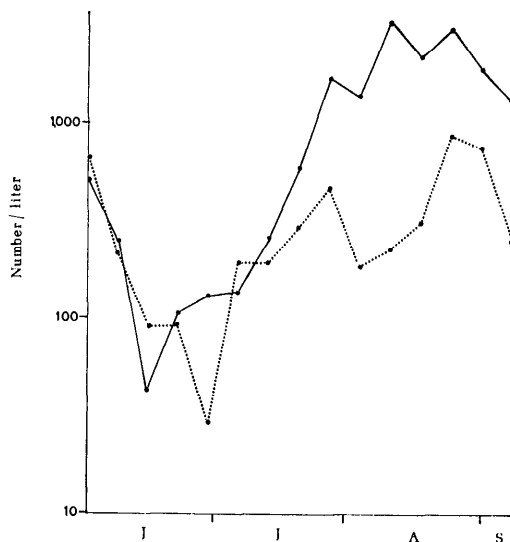FIG. 28. Mean numerical densities of *Chydorus* in ponds with and without fish in 1967 (F ——, WF · · ·).

FIG. 30. Mean numerical densities of rotifers in ponds with and without fish in 1967 (F ——, WF · · ·).
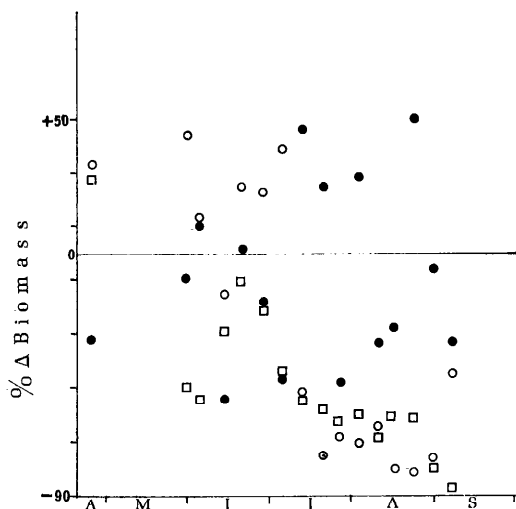
FIG. 31. Mean percent difference of zooplankton biomass between ponds with and without fish expressed as $[(F - WF)/(F + WF)] \times 100$ at three nutrient levels (HN = ●, MN = □, LN = ○).

FIG. 32. Mean biomass of total zooplankton in ponds with and without fish at HN in 1967 (F ——, WF · · ·).

total biomass was always less in the ponds with fish. Again, the differences were most pronounced in late summer. But under HN conditions fish predation appeared to have no effect on the standing biomass of zooplankton. The predominant contribution of HN ponds to the analysis across all nutrient levels thus accounts for the lack of any evidence of a predation effect (Fig. 32).

The impact of predation on the mean contribution of *Ceriodaphnia* was equally pronounced at LN (1% with fish vs. 56% without fish), MN (3% vs. 58%), and HN (4% vs. 44%) levels. Other species show several nutrient–predation interactions (Figs. 33 and 34). *Bosmina* was abundant in the presence of fish but restricted to LN and MN levels. *Chydorus* contributed 27% and 12% of the biomass in HN and MN ponds with fish, but it was scarce (4%) in LN ponds.

In the absence of fish, HN ponds in late summer exhibited a relatively equitable species distribution, somewhat resembling the HN conditions in ponds with fish. This phenomenon may be related to the growth and dominance of macrophytes or blue-
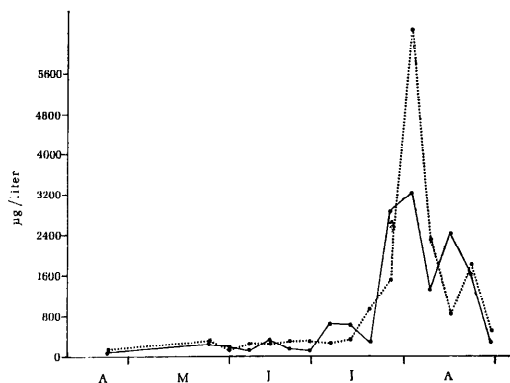
green algae in these ponds. The LN and MN ponds without fish repeated the pattern of previous years, in which *Ceriodaphnia* dominated.

Production

Four crustacean species, plus rotifers, contributed significantly to production in 1967 and were analyzed individually before total zooplankton production was considered (Table 14).

Fish reduced *Ceriodaphnia* production drastically, especially at LN and MN levels. *Ceriodaphnia* demonstrated no nutrient effect by itself, although a possible interaction with predation is suggested at HN levels. Total rotifer production was over 10 times greater in HN ponds than at the two lower nutrient levels. Mean production was higher in ponds with fish but was not statistically significant. *Simocephalus* production (based on net samples) occurred almost exclusively in HN ponds, and the presence of fish appeared to have no effect. The independent dip-jar sampling program for *Simocephalus* biomass followed the same pattern. Although we ran field life tables with *Chydorus*, survival was low and growth rate estimates are not good. However, the estimates of egg development times (2.0 days) and maturation time (4.5 days) are in agreement with
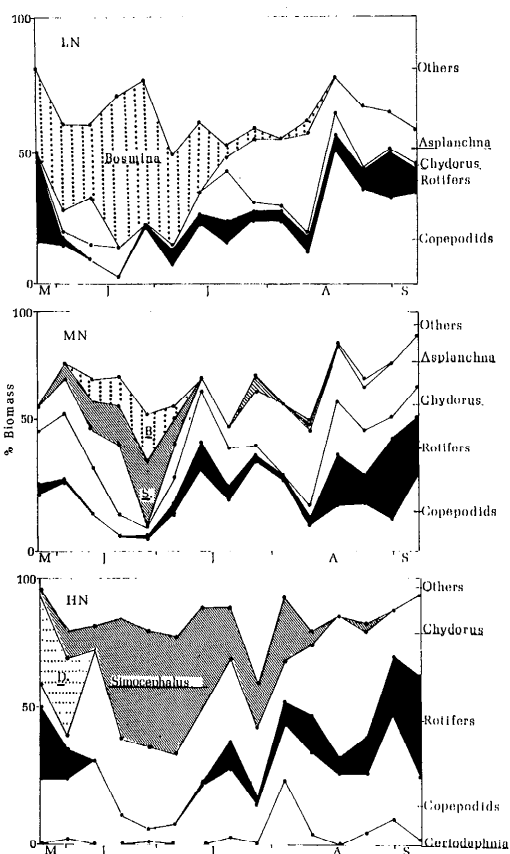
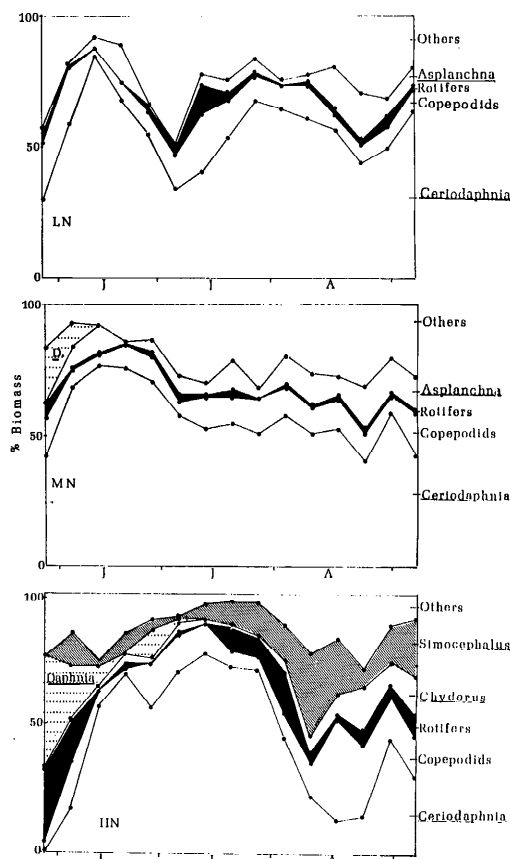FIG. 33. Mean percent species composition of zooplankton biomass in ponds with fish at three nutrient levels.

FIG. 34. Mean percent species composition of zooplankton biomass in ponds without fish at three nutrient levels.

those of Keen (1967) for *Chydorus sphaericus* at 25C. *Chydorus* production was significantly higher at HN levels but did not differ significantly across predation levels.

No growth rate estimates were available for *Bosmina*; an egg development time of 2.0 days and a maturation time of 3.5 days (as with *Ceriodaphnia*) were used arbi-

TABLE 14. *Zooplankton production estimates* ($\overline{X} \pm$ SE) *expressed as μg/liter dry wt for summer 1967 and percent contribution of dominant species*

	Total production	Ceriodaphnia (%)	Rotifers (%)	Simocephalus (%)	Chydorus (%)	Bosmina (%)
HN	11,823 ± 3,073	3,735 ± 1,151 (32)	2,018 ± 638 (17)	2,752 ± 1,539 (23)	3,318 ± 1,222 (28)	0 (0)
MN	3,034 ± 970	2,584 ± 1,095 (85)	128 ± 35 (4)	64 ± 29 (2)	104 ± 57 (3)	154 (5)
LN	3,412 ± 648	2,045 ± 907 (60)	154 ± 41 (5)	10 ± 4 (0)	30 ± 16 (1)	1,173 (34)
F	4,793 ± 1,678	662 ± 377 (14)	1,046 ± 556 (22)	669 ± 442 (14)	1,501 ± 769 (31)	915 (19)
WF	7,397 ± 2,312	4,915 ± 496 (66)	465 ± 177 (6)	1,216 ± 1,087 (16)	801 ± 767 (11)	0 (0)
HNF	10,835 ± 2,026	1,800 ± 852 (17)	2,887 ± 1,082 (27)	1,879 ± 1,114 (17)	4,269 ± 1,158 (39)	0 (0)
IINWF	12,815 ± 6,495	5,670 ± 1,467 (44)	1,151 ± 245 (9)	3,626 ± 3,135 (28)	2,368 ± 2,285 (19)	0 (0)
MNF	913 ± 360	146 ± 48 (16)	128 ± 72 (14)	121 ± 32 (13)	186 ± 96 (20)	332 (36)
MNWF	5,180 ± 210	5,022 ± 215 (97)	129 ± 31 (2)	6 ± 3 (0)	23 ± 10 (0)	0 (0)
LNF	2,618 ± 1,172	39 ± 25 (1)	156 ± 52 (6)	6 ± 3 (0)	47 ± 31 (2)	2,370 (90)
LNWF	4,258 ± 239	4,052 ± 301 (95)	179 ± 76 (4)	15 ± 7 (0)	12 ± 6 (0)	0 (0)

trarily in estimating its production. *Bosmina* was abundant in 3 ponds (2 LN and 1 MN), all of which contained fish. It contributed a large share of the production in these ponds.

The sum of the species production estimates is given as total zooplankton production in Table 14. Production values at LN and MN levels were similar and significantly ($p = 0.05$) lower than at HN levels. Predation levels did not show significant differences.

The percentage breakdown of total production is also listed in Table 14. At HN levels, *Chydorus*, *Ceriodaphnia*, rotifers, and *Simocephalus* all contributed large portions of the production. Rotifers and *Chydorus* dominated production in ponds with fish and *Ceriodaphnia* prevailed in the absence of fish, especially at the two lower nutrient levels. *Bosmina* accounted for nearly the entire production in LN ponds with fish. Rotifer production averaged 3 times greater in the presence of fish.

Summary

Total zooplankton standing crops were similar at LN and MN levels and much greater in the HN ponds. *Ceriodaphnia* was dominant in all ponds without fish. The species composition in HN ponds may have been affected by the dominance of aquatic vascular plants, since *Simocephalus* and *Chydorus* (both weed dwellers) contributed strongly to their total biomass. Fish predation had no effect on total biomass but a strong impact on species composition. *Ceriodaphnia* was all but annihilated by the fish, but the smaller *Chydorus*, *Bosmina*, rotifers, and miscellaneous crustaceans increased in their presence. The larger *Simocephalus* was affected little by fish predation. Production estimates reveal the same patterns.

The data show an interaction of nutrients and predation. At LN and especially MN levels, zooplankton biomass was nearly always greatest in ponds without fish, although at HN levels fish had no effect. Thus, the impact of fish predation must be treated as a function of nutrient level.

BENTHOS

Methods

Triplicate samples of the benthic fauna were taken with a modified 15-cm Eckman dredge mounted on a pole (Anderson and Hooper 1956) each week from June to September and occasionally during spring and fall. Distribution of the samples within a pond was determined by random selection of 3 quadrats from a 9-unit grid system, and on each date, a new set of quadrats was randomly chosen for each pond. The dredge samples a 232-cm^2 area of the bottom surface with a penetration from 5 to 10 cm depending on the substrate.

The sampling procedure took 3 days. Ponds 21 through 27 were sampled on Tuesday, ponds 28 through 34 on Wednesday, and ponds 35 through 40 on Thursday of each week. The samples were collected from 0800 to 1000 hours and sorting completed by 1530. Each week 60 samples were taken (total, 2,820): 840 in 1965, 1,020 in 1966, and 960 in 1967. Equal numbers of samples per pond were taken each year.

Samples were brought in plastic buckets to the laboratory. Each was washed through a No. 60 brass sieve of the Tyler series having a mesh size (0.246 mm) small enough to retain the early instars of benthic species. We then extracted the animals from the remaining debris by a flotation technique (Anderson 1959) using a saturated sugar solution and a small amount of glacial acetic acid. This method is 90–99% efficient with benthic insects and crustaceans (Gerking 1962; Cooper 1965). Animals were preserved in 95% alcohol until further sorting. Some 29 benthic invertebrate taxa were counted and the data punched on computer cards.

Emergent insects were collected on Monday and Friday from June until September. The traps consisted of cylindrical metal frameworks (106.7 cm high, 182.9 cm circumference) covered with aluminum window-screening. The bottom edge of the frame rested in the substrate; the upper edge was about 15 cm below the water surface. A nylon organdy top was sus-

TABLE 15. *Benthic species list and dry weights (mg)*

Taxa	Category		Dry wt (mg)	Taxa	Category		Dry wt (mg)
Diptera				Ephemeroptera			
Chironomus tentans	Instar	1	0.005	*Caenis simulans*	0–1 mm		0.010
		2	0.04		1–2		0.044
		3	0.45		2–3		0.130
		4	1.30		3–4		0.320
	Pupae		2.10		4–5		0.573
Glyptotendipes sp.	Instar	1	0.005	*Callibaetis ferrugineus*	0–1 mm		0.02
		2	0.02		1–2		0.05
		3	0.15		2–3		0.08
		4	0.45		3–4		0.14
Microtendipes sp.	Instar	1	0.005		4–5		0.31
		2	0.01		5–6		0.63
		3	0.02		6–7		0.85
		4	0.10		7+		1.68
Ablabesmyia	0–1 mm		0.005	Trichoptera	1–3 mm		0.026
	1–2		0.007		3–5		0.074
	2–3		0.010		5+		0.768
	3+		0.060	Amphipoda			
Procladius sp.	1–2 mm		0.007	*Hyalella azteca*	0–1 mm		0.015
	2–3		0.01		1–2		0.036
	3–4		0.02		2–3		0.080
	4+		0.035		3–4		0.133
Tanytarsini	1–2 mm		0.007		4–5		0.20
	2–3		0.01		5–6		0.41
	3–4		0.02		6+		0.60
	4+		0.035	Dytiscidae	Instar	1	0.04
Corynoneura sp.	1–2 mm		0.007			2	0.17
Ceratopogonidae	0–5 mm		0.025			3	0.97
	5–10		0.14	Zygoptera	0–5 mm		0.35
	10–15		0.26		5–10		2.19
Chironomus s.s.	Instar	2	0.007		11–15		5.83
		3	0.20	Corixidae	0–10 mm		0.60
		4	1.50				
Misc. Diptera	0–1 mm		0.005	Haliplidae	0–5 mm		0.47
	1–2		0.007		5+		0.94
	2–3		0.01	*Hirundinea*	0–10 mm		1.43
	3–4		0.02		10+		5.70
	4–5		0.04	Hydrophilidae	0–5 mm		1.04
	5–6		0.065		5–10		2.14
	6+		0.150		10–15		4.42
	Pupae		0.100				

pended from an extension of the metal framework and tied around the top of the cylinder. Insects in the nylon bag and floating on the water were preserved in alcohol. The traps were relocated at random on each collecting date. There was only a single trap per pond, so the subsample variability is estimated from the duplicate samples per week, resulting in an error term with both a spatial and a temporal component. The long and variable period of 3 or 4 days between collections probably added some time-differential mortality to the temporal component. In general, these data should be considered only a relative measure illustrating emergence patterns in the ponds.

Animals of each species and size category from all ponds, freshly collected, were oven-dried at 70C and weighed to convert

TABLE 16. *List of emergent insects and their dry weights (mg)*

Taxa	Dry wt (mg)
Chironomus tentans	1.22
Glyptotendipes sp.	0.85
Ablabesmyia	0.154
Misc. Diptera	0.146
Callibaetis ferrugineus	1.25
Caenis simulans	0.154
Misc. Trichoptera	0.06
Polycentropis	0.91
Zygoptera	5.61
Phryganea	18.05
Chaoborus	0.75

numbers to biomass (Table 15). Biomass of emergent insects was calculated from dry weights of alcohol-preserved samples (Table 16). Large differences between late larval and adult dry weights are due to the size distribution of larvae in the samples. For instance, the majority of our *Ablabesmyia* larvae had a body length slightly over 3 mm, but they would have grown to 5 or 6 mm before emergence. The conversion factor for body length to biomass is thus weighted by this skew toward smaller animals in the samples for the 3-mm+ category.

For estimates of generation times, eggs of a variety of benthic organisms were collected from the ponds and the larvae cultured at 23C with an abundance of food. *Chironomus tentans* was a dominant species and easily cultured, so it was selected for experiments to determine the influence of food quantity on individual growth rates and generation times. The cultures (45) were started in 7.5-liter glass aquaria, each stocked with about 1,000 eggs from laboratory populations. Sediments from an old fishtank culture were added in equal amounts to all 45 tanks. Light, temperature, and aeration were uniform. The amount of food added per unit time was proportional to the average body weight of *C. tentans* larvae during each time interval. We chose nine arbitrary food levels by assuming 30, 50, and 70% survival of the initial cohort of 1,000 until emergence

and then adding nutrients at 1, 5, and 10× the estimated standing crop of midge larvae. These values were obtained from a pilot experiment using a moderate food level. The amount of food required was estimated for consecutive 5-day intervals and a fifth of this was added daily. At day 3 and at 5-day intervals thereafter, 15 larvae were sampled at random from each tank and measured. Adults were collected daily from each tank, and body length and fecundity were measured.

Results 1965–1966

Nutrients

Laboratory. Laboratory experiments indicate an inverse relationship between food level and generation time for *C. tentans* (Fig. 35). Animals at low food levels required at least 18 days to reach the fourth instar at 23C, but only 8 days at high food levels. The duration of the first instar was 8 days at low food and 3 at high. This same pattern is apparent in the second and third instars.

Highest emergence rates over a 40-day period were obtained at higher food levels, also indicating a reduced generation time (Table 17). Percent emergence per day was computed from the ratio of emergent to total living animals for each population. Total number is the sum of the animals removed, the number of emergent adults, and the number of larvae still living at 40 days. Survivorship of the initial 1,000 eggs (Table 17) is not affected by food level and thus cannot account for the relationship between nutrient level and generation time.

The size of the adult is also related to nutrient level. At low food levels, the fourth instar larvae averaged 15.2 mm long. Adults averaged 6.5 mm and produced 500 eggs in a single brood. At high food levels, the fourth instar larvae averaged 19.9 mm, and adults were 8.5 mm and laid about 1,800 eggs. None of the adult *C. tentans* collected in the field was as small as those produced at the low food levels in the laboratory.
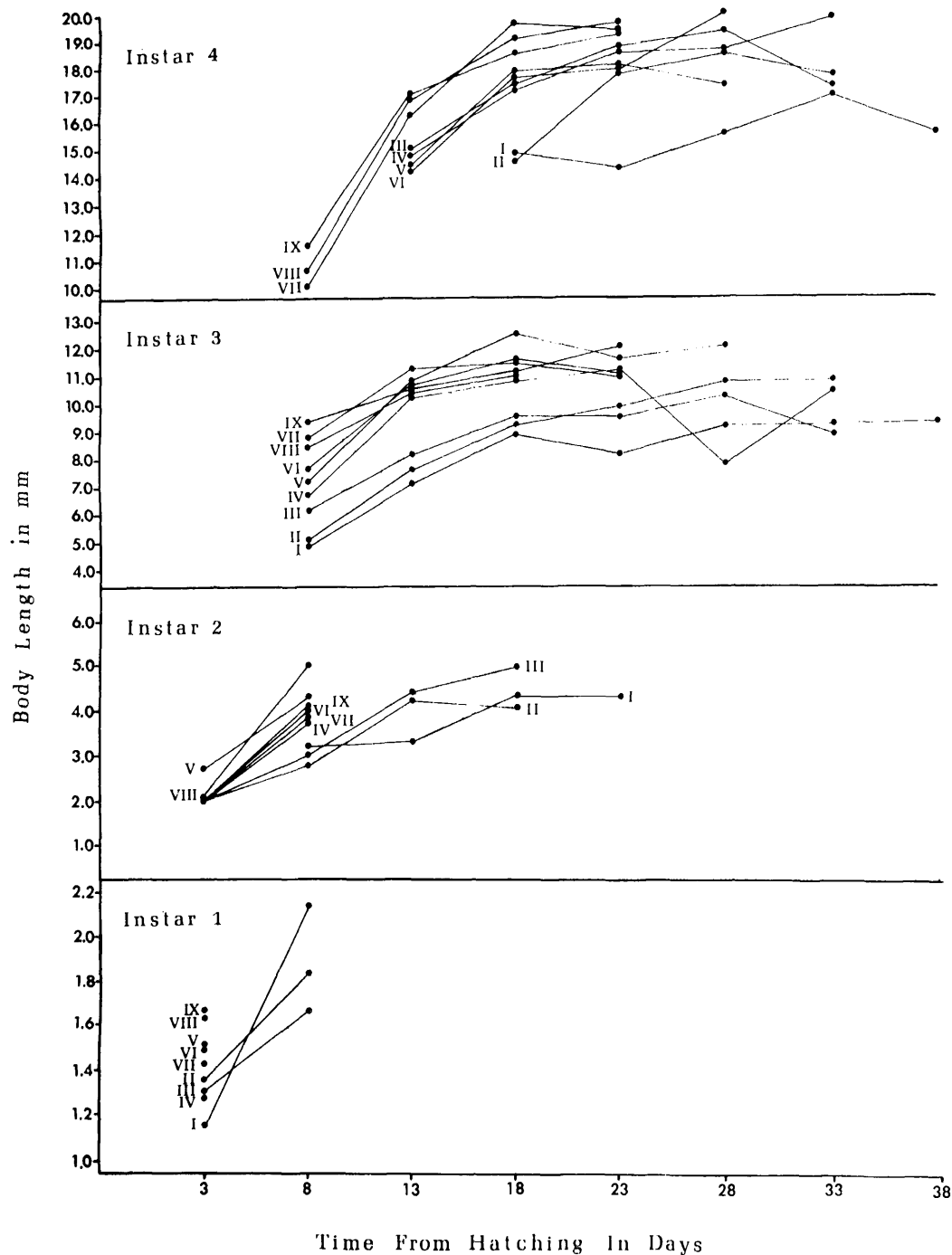
FIG. 35. Mean body lengths of *Chironomus tentans* larvae at various ages in laboratory growth experiments. Animals were cultured at nine food levels at 23C. Food levels ranged from low (I) to high (IX).

TABLE 17. *Laboratory experiment:* Chironomus tentans

Food level	Total surviving (%)		Emerging/day (%)	
	$\bar{x}$	SE	$\bar{x}$	SE
I	27.1	3.0	0.112	0.036
II	16.6	2.2	0.302	0.056
III	28.2	3.0	0.440	0.075
IV	16.5	3.5	1.766	0.285
V	28.8	2.2	0.927	0.299
VI	31.7	4.3	1.614	0.249
VII	19.6	5.3	1.261	0.197
VIII	24.0	7.4	2.033	0.844
IX	36.3	6.6	1.120	0.380

Total biomass. Total standing crop of benthic invertebrates in 1965 was directly related to nutrient level (Fig. 36). Following nutrient addition, the benthic fauna increased in biomass until late September. From mid-June to late August, the biomass increased both by recruitment and by growth; after August, there was no further recruitment of first instar organisms, and the increase in biomass was due to individual body growth.

The increase in biomass in the LN ponds also results from individual growth, especially in the latter portion of summer, and increased recruitment. Insect egg input was an uncontrollable element in the experimental system. In particular, *C. tentans* recruitment into the LN ponds was
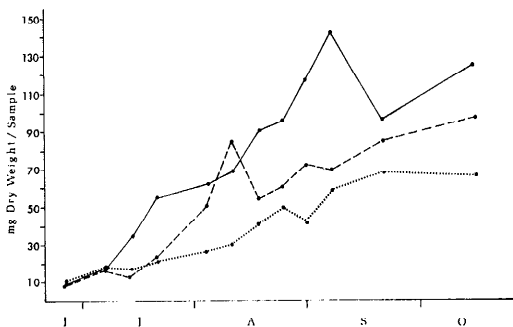

FIG. 36. Mean total benthic biomass per sample at three nutrient levels in 1965 (HN ———, MN – – –, LN · · ·). Average standard errors are 14.0, 27.4, and 25.2 mg in LN, MN, and HN ponds.
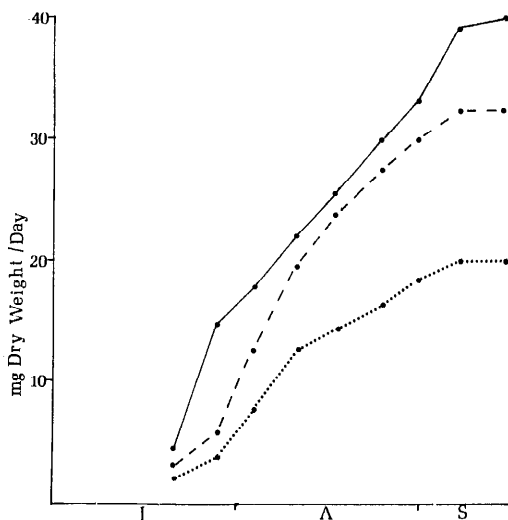

FIG. 37. Cumulative weekly estimates of emergence rates expressed as mg dry wt trap^{-1} day^{-1} at three nutrient levels in 1965 (HN ———, MN – – –, LN · · ·).

probably raised above its expected level by the reproductive activity of adults from the adjacent HN ponds.

The biomass of emergent insects per trap-day was variable, due partly to fluctuations of weather and of duration of the sampling period. There was considerable mortality within the traps, including some predation by adult odonates. Nevertheless, the emergence data reflect the basic pattern of response of the benthic community to nutrient input. Enriched ponds consistently showed higher emergence rates (Fig. 37). But emergence after mid-September had little impact on the aquatic community since there was no further observed recruitment of first instar organisms.

In 1966, the biomass in spring (Fig. 38) reflected the nutrient level effects observed the preceding October (Fig. 36). During summer, the standing crops in LN and MN ponds fluctuated around 35-mg dry wt/ sample, as in spring. In HN ponds, however, the biomass decreased steadily until mid-August and then rose. During the entire period from June through early September, emergence was continuous at all three nutrient levels (Fig. 39). The rates
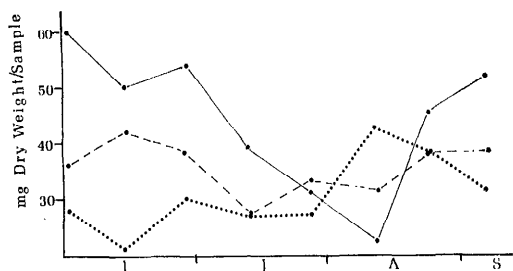
FIG. 38. Mean biomass per sample of benthic fauna at three nutrient levels in 1966 (HN ——, MN – – –, LN · · ·). Average standard errors are 8.6, 7.9, and 15.5 mg in LN, MN, and HN ponds.

were again directly related to the nutrient input.

Community response. The benthic community was composed primarily of: Diptera —*C. tentans, Procladius* sp., *Ablabesmyia* sp., Tanytarsini, *Glypotendipes* sp., *Microtendipes* sp., Ceratopogonidae, and *Chironomus* sp.; Trichoptera—*Ocetis* sp. and *Polycentropis* sp.; Ephemeroptera—*Caenis simulans* and *Callibaetis ferrugineus*; Zygoptera—*Ishneura* sp. and *Enallagma* sp.; Anisoptera—*A. junius,* Libelludidae, and Gomphidae; Amphipoda—*Hyalella azteca.* (Species identified by K. W. Cummins and A. L. Hamilton.)

The composition of the benthic community was related to the experimental manipulations, most markedly in the relative biomass of the two dominant organisms, *C. tentans* and *C. simulans.* Nutrient level
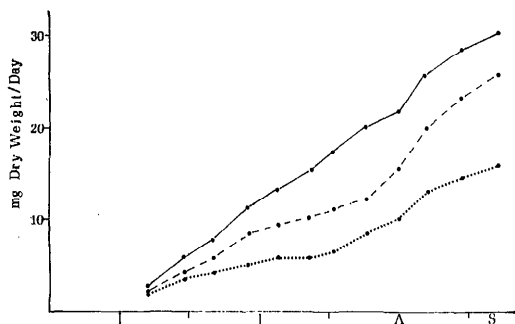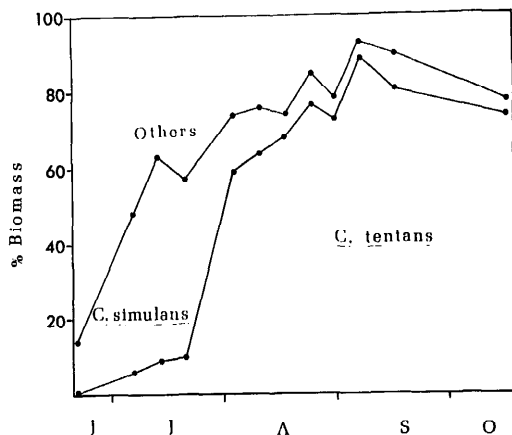

FIG. 40. Mean percent biomass per sample at HN in 1965. Average standard errors are 9.9% for *Chironomus tentans* and 8.4% for *Caenis simulans.*

in 1965 affected *Chironomus* directly and *Caenis* inversely; by August, *Chironomus* constituted about 80% of the biomass in the HN ponds and *Caenis* accounted for 5% (Fig. 40). Under LN conditions, *Caenis* averaged about 40% of the biomass and *Chironomus* about 25% (Fig. 41). No other taxon contributed more than 10%.

The most striking change in the benthic community between 1965 and 1966 was in the dominance of *Chironomus* (Figs. 42 and 43). In early June 1966, *Chironomus* contributed 76% of the biomass in HN, 46% in MN, and 41% in LN ponds. These

FIG. 39. Cumulative weekly estimates of emergence rates expressed as mg dry wt trap^{-1} day^{-1} at three nutrient levels in 1966 (HN ——, MN – – –, LN · · ·).
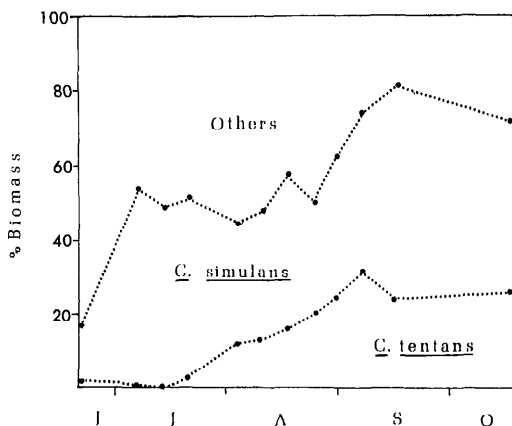

FIG. 41. Mean percent biomass per sample at LN in 1965. Average standard errors are 10.8% for *Chironomus tentans* and 4.4% for *Caenis simulans.*
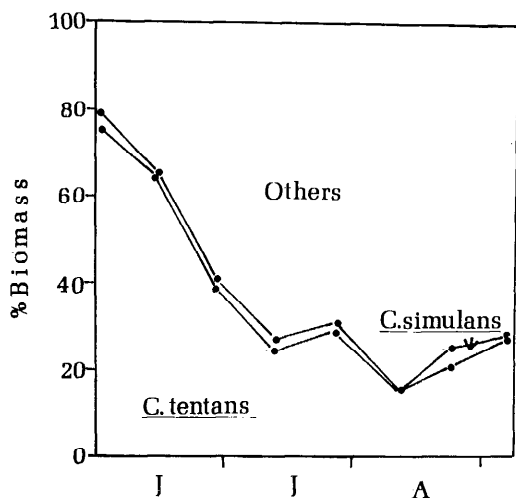
FIG. 42. Mean percent biomass per sample at HN in 1966. Average standard errors are 5.9% for *Chironomus tentans* and 2.2% for *Caenis simulans*.
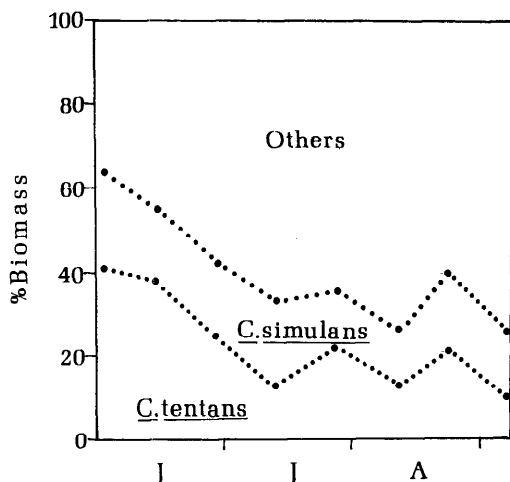
FIG. 43. Mean percent biomass per sample at LN in 1966. Average standard errors are 3.7% for *Chironomus tentans* and 4.4% for *Caenis simulans*.

values reflect the 1965 response; the composition by weight of the benthos did not change over the winter. But *Chironomus* declined during summer to levels of <30% at HN and 20% at MN and LN levels. These values are less than half those of 1965. *Caenis* contributed up to 50% of the biomass in LN and MN ponds in 1965 and about 20% in 1966. At HN levels *Caenis* never accounted for more than 4%. Total community biomass, in general, also declined in 1966.

The composition of the category designated as "others" is diverse. No single taxon contributed more than 8% of the biomass, which was distributed uniformly among eight taxa—all small-bodied animals.

Body size. Community indices have traditionally been taxonomically oriented. Many benthic invertebrates are omnivorous and size specific in their feeding habits; an alternative mode of examining community structure might be based on body size. The responses of the benthic community to our manipulations clearly show shifts in the abundance of organisms characterized only by their body weight.

All animals were placed in one of four size classes: <0.01-, 0.01–0.10-, 0.10–1.0-, and >1.0-mg dry wt, using average figures

from Table 15. This procedure will not distinguish certain species at times during their life history (e.g., second instars of *C. tentans* will be grouped with late instar Tanytarsini, as both are included in the 0.01–0.10-mg range). After the decline of general recruitment in late August, however, individual species will become more distinct as size differences are accentuated by the accumulation of later instars. The responses of the smaller species should be more evident then because instar and species abundances are not as confounded.

In 1965, the smallest category (<0.01 mg) constituted about 9% of the benthic standing crop in June at all three nutrient levels (Fig. 44); by late summer this had decreased to about 2%. The decrease was most rapid and consistent in HN ponds. The next size range at HN also declined—to 10% of the biomass by late summer, although fluctuating around 45% at LN. The relative contribution of the 0.10–1.0-mg category was not clearly related to the fertilization regime. But the largest size category is directly related to nutrient input and constituted up to 65% of the biomass in the HN ponds. The relationship of nutrient level and body size distribution thus seems to pivot on the 0.10–1.0-mg range.
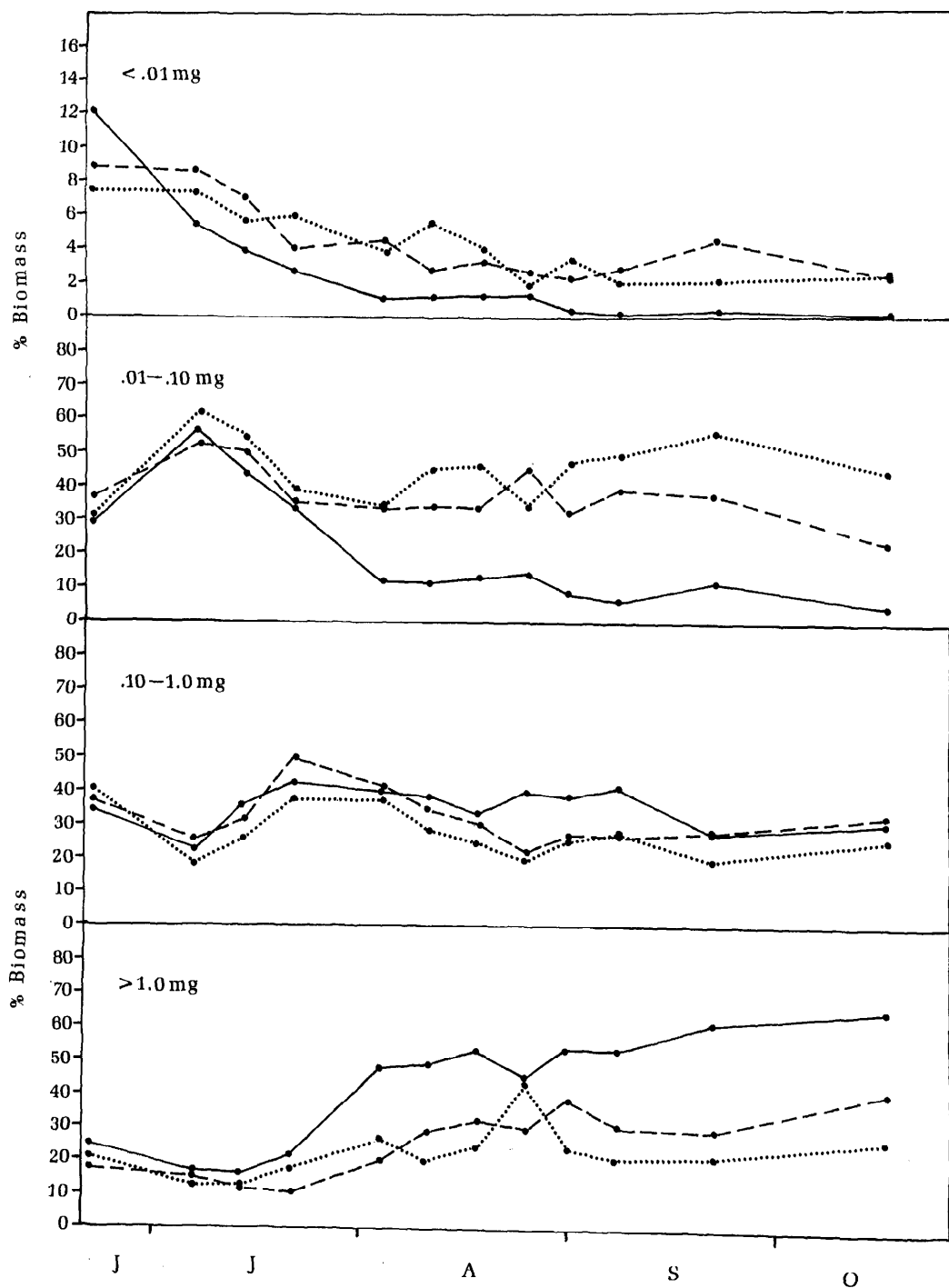
FIG. 44.   Mean percent biomass per sample at three nutrient levels in 1965. Animals are divided into four body-size categories based on dry weights (HN ——, MN – – –, LN · · ·).
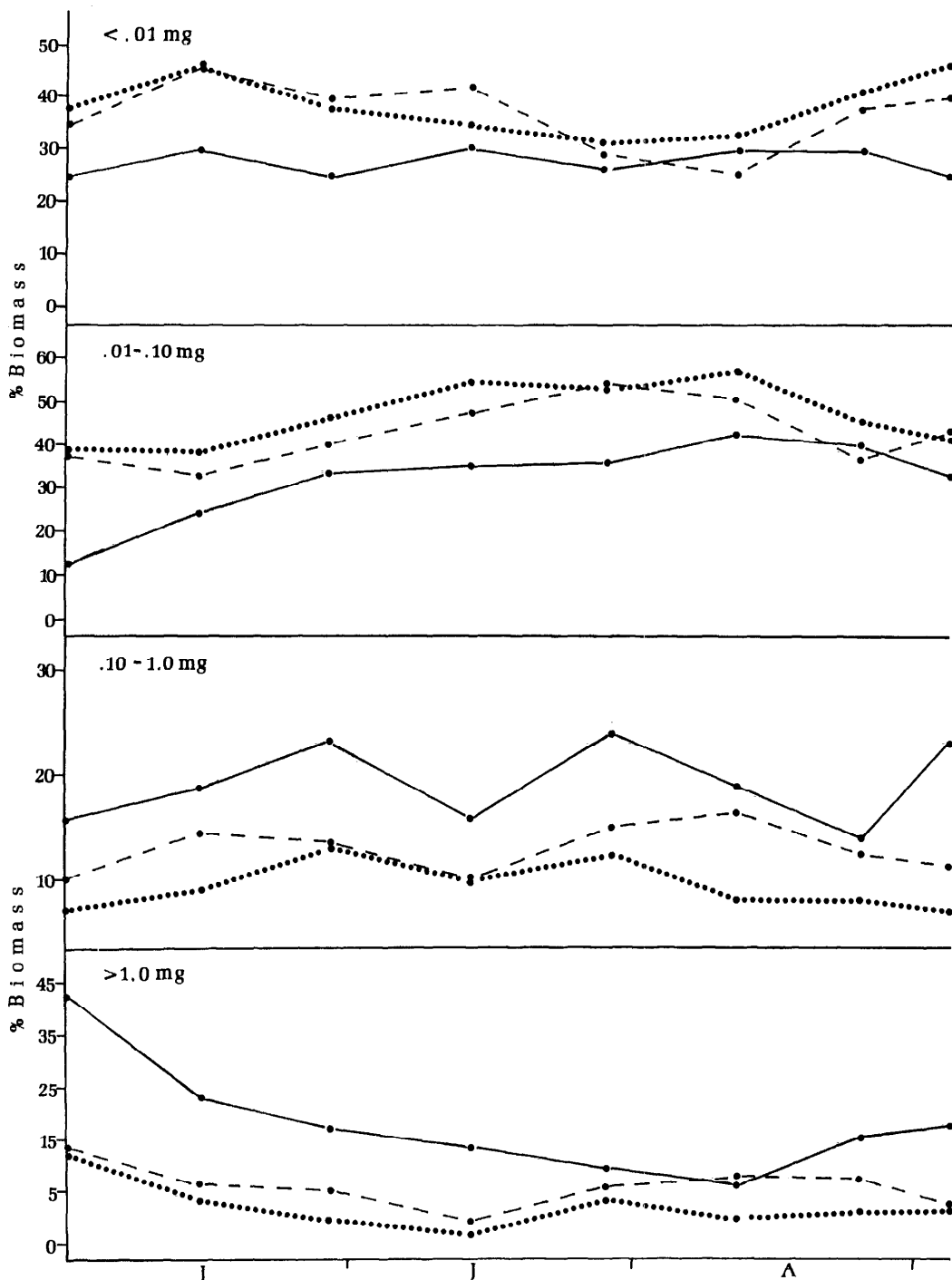
FIG. 45. Mean percent biomass per sample of benthic organisms classified by body size at three nutrient levels in 1966 (HN ——, MN – – –, LN · · ·).

FIG. 46. Frequency of benthic samples in 1965 containing given numbers of organisms with individual body weights <0.01-mg dry wt (HN, dots; MN, closed circles; LN, solid black).

Small animals were more abundant and contributed a significantly larger proportion of the biomass in 1966 (Fig. 45), when the smallest size constituted from 30 to 40% of the biomass at all nutrient levels. At HN this is about a 10-fold increase over 1965. There is only a slight indication of a nutrient effect, with small organisms contributing the least under HN conditions. The 0.01–0.10-mg size range encompassed about 40% of the standing crop at all nutrient levels in 1966, as it did at LN and MN levels in 1965. The larger two size categories reflected the 1965 pattern, but with a much reduced contribution to the total standing crop. These two categories in 1966 ranged from 10–20% in LN, 12–25% in MN, and 27–62% in HN ponds. In 1965, the range of estimated values was 40–60% in LN, 40–70% in MN, and 35–95% in HN ponds.

Size-frequency distribution. The sampling procedure for the benthic fauna provided a large number of randomly distributed 232-cm² samples. The frequencies with which these samples contained organisms in the specific body-size categories represent the probability that a predator would encounter various densities of prey of differing body size—an important characteristic of the environment for the predator population. The latter part of summer 1965 was selected for this analysis, after the fauna had responded to nutrient manipulation. Organisms with body weights <0.01 mg have equal probabilities of a given numerical abundance in LN and MN ponds (Fig. 46). The densities of small organisms in the samples from HN ponds is skewed toward lower values.

The distribution for large organisms (>1.0 mg) is skewed toward low numbers in LN ponds (Fig. 47), but it is somewhat more uniform at HN levels. No samples
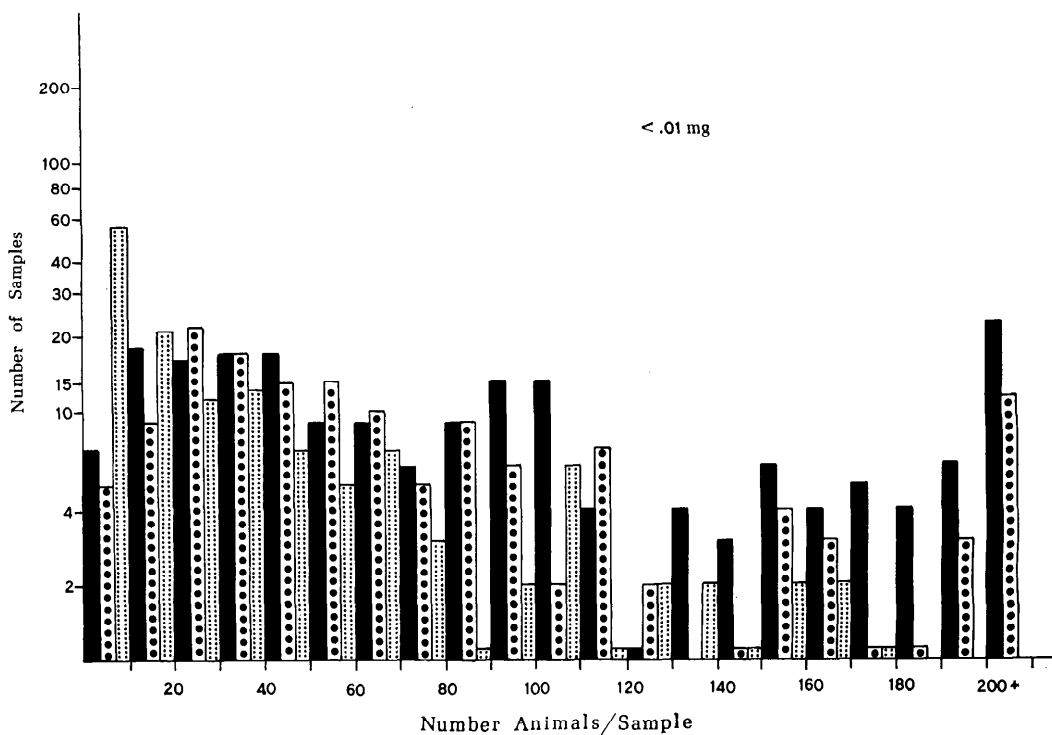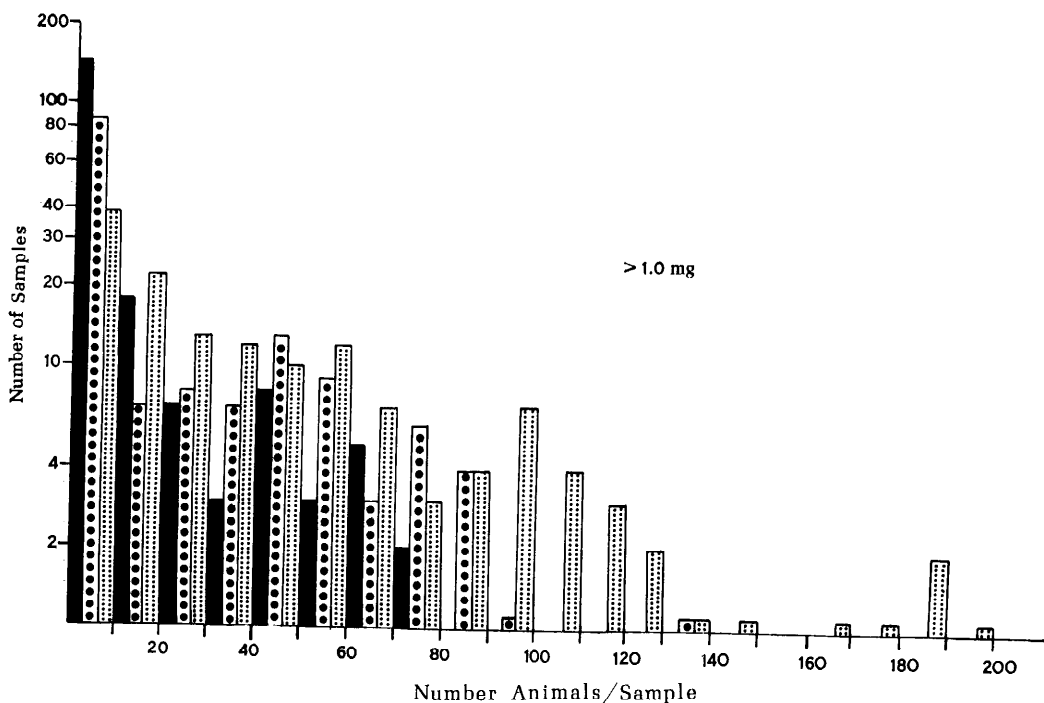
FIG. 47. Frequency of benthic samples in 1965 containing given numbers of organisms with individual body weights > 1.0-mg dry wt (HN, dots; MN, closed circles; LN, solid black).

contained more than 70 animals larger than 1.0 mg in LN ponds; fewer than 10 were found in 145 samples. In HN ponds, some samples had more than 180 large prey organisms. The distribution at MN falls between these extremes. The 1966 data demonstrate similar trends.

The addition of nutrients thus altered the frequency distribution of different size prey organisms, producing more contagious distributions of large prey under HN conditions. These shifts in frequency result from changes in densities and spatial distributions. There is no direct evidence available to separate the two since we made no independent measurements of spatial distribution.

Population response. Detailed analyses of the dominant species *C. tentans* and *C. simulans* provide the demographic estimates, required for the production models presented later, of instar duration, survivorship, and life-history patterns.

In 1965 we were able to measure the

impact of differential birth, growth, and death rates on the demographic properties of *C. tentans.* Two weeks after the first nutrient manipulation, the density of first instar *Chironomus* increased in the HN ponds (Fig. 48). High recruitment rates, measured as the abundance of first instar larvae, continued through the last week in August and then decreased sharply. First instar duration was about 3 days. The same pattern was apparent in the MN and LN ponds, but the rates were lower.

Second instar animals increased later in July and decreased later in September. The second instar lasted longer (mean of 4 days at summer temperatures), so the numerical response appeared greater than that of the first instar. Instar duration is also affected by nutrient level (*see* Fig. 35), which confounds the response by reducing the differences in numerical standing crops at the three nutrient levels. *Chironomus* in HN ponds will have shorter generation times and, therefore, lower standing crops at
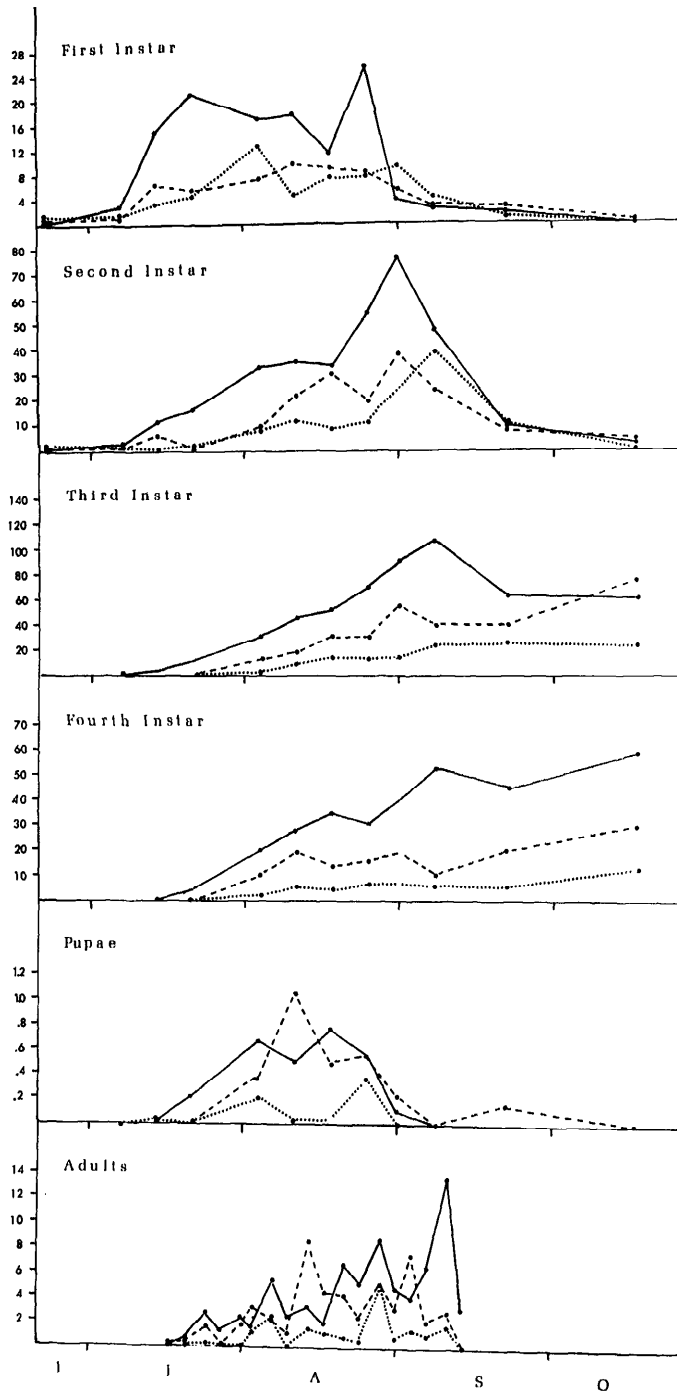
FIG. 48.   Mean densities of the life-history stages of *Chironomus tentans* at three nutrient levels in 1965 (HN ———, MN – – –, LN · · ·). Adults counted as No. trap⁻¹ day⁻¹; all others as No./sample.
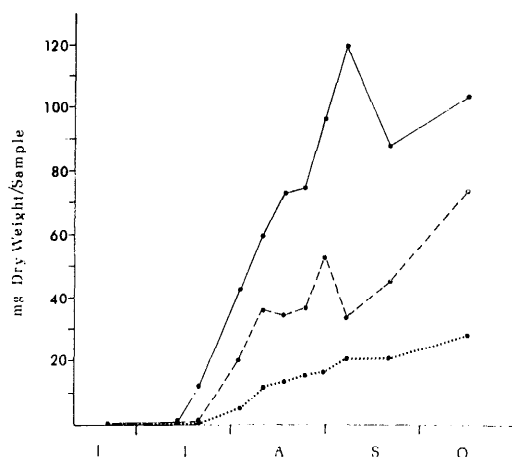
FIG. 49. Mean biomass per sample of *Chironomus tentans* at three nutrient levels in 1965 (HN ——, MN - - -, LN · · ·). Average standard errors are 10.9, 21.2, and 23.9 mg in LN, MN, and IIN ponds.

FIG. 50. Mean biomass per sample of *Chironomus tentans* at three nutrient levels in 1966. (HN ——, MN - - -, LN · · ·). Average standard errors are 7.0, 6.0, and 12.9 mg in LN, MN, and IIN ponds.

any given temperature per unit numerical increase.

Third instars increased from late July until mid-September. During this period, densities higher than those of earlier instars were again due to the extended developmental period (about 9 days). Fall accumulation of this instar, which constitutes about 50% of the overwintering population, is due to the reduced growth rates in late September and October. The fourth instar was similar in pattern to the third but lagged about 15 days behind the numerical increase of the first instar at HN levels. The lag time at MN and LN was estimated at 25 and 50 days respectively. Third and fourth instars both increased continuously through October, skewing the size distribution toward large individuals.

Densities of pupae and the emergence rates (Fig. 48) indicate the turnover of *Chironomus* populations at each nutrient level; larval instars do not indicate turnover rates, since several generations of animals coexist at one time. Emergence rates increased at HN about 23 days after the increase in first instar. Adults bred within 2 days and supported the continuous recruitment through early September. Emergence rates increased at the higher nutrient levels.

In 1966 *Chironomus* recruitment was maximal in June but continued at a constant low rate during summer. The abundance of the first instar reflects this at all three nutrient levels. The second instar was also most abundant in June, with similar temporal patterns at each nutrient level. This stage was present in constant numbers for the remainder of summer. Third instars increased gradually during summer with no apparent differences between nutrient levels until early September, when they increased in HN ponds as in 1965. The fourth instar was more abundant in HN than in LN or MN ponds in early June—a residual effect of 1965. Abundances dropped consistently in HN ponds until mid-August and then gradually increased in a pattern similar to that of third instars. The densities remained constant in LN and MN ponds. The numbers of pupae and emergent adults indicated a continuous population turnover during summer. In LN and MN ponds, maximum emergences were in early and late summer; in IIN ponds, emergence was more continuous.

The patterns in standing crop biomass of *C. tentans* follow the abundance of fourth instar larvae. The increased biomass in HN ponds in 1965 (Fig. 49) persisted through early June 1966 (Fig. 50), after which it decreased uniformly until early August and

FIG. 51. Mean densities of life-history stages of *Caenis simulans* at three nutrient levels in 1965 (HN ——, MN – – –, LN · · ·). Adults counted as No. trap⁻¹ day⁻¹; all others as No./sample.

FIG. 51. Mean densities of life-history stages of *Caenis simulans* at three nutrient levels in 1965 (HN ——, MN – – –, LN · · ·). Adults counted as No. $trap^{-1}$ day^{-1}; all others as No./sample.

FIG. 52. Mean densities of life-history stages of *Caenis simulans* at three nutrient levels in 1966 (HN ——, MN – – –, LN · · ·). Adults counted as No. trap^{-1} day^{-1}; all others as No./sample.
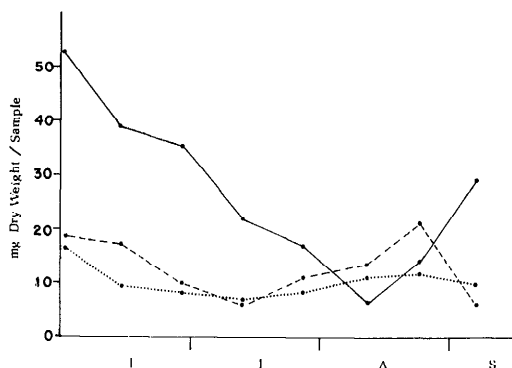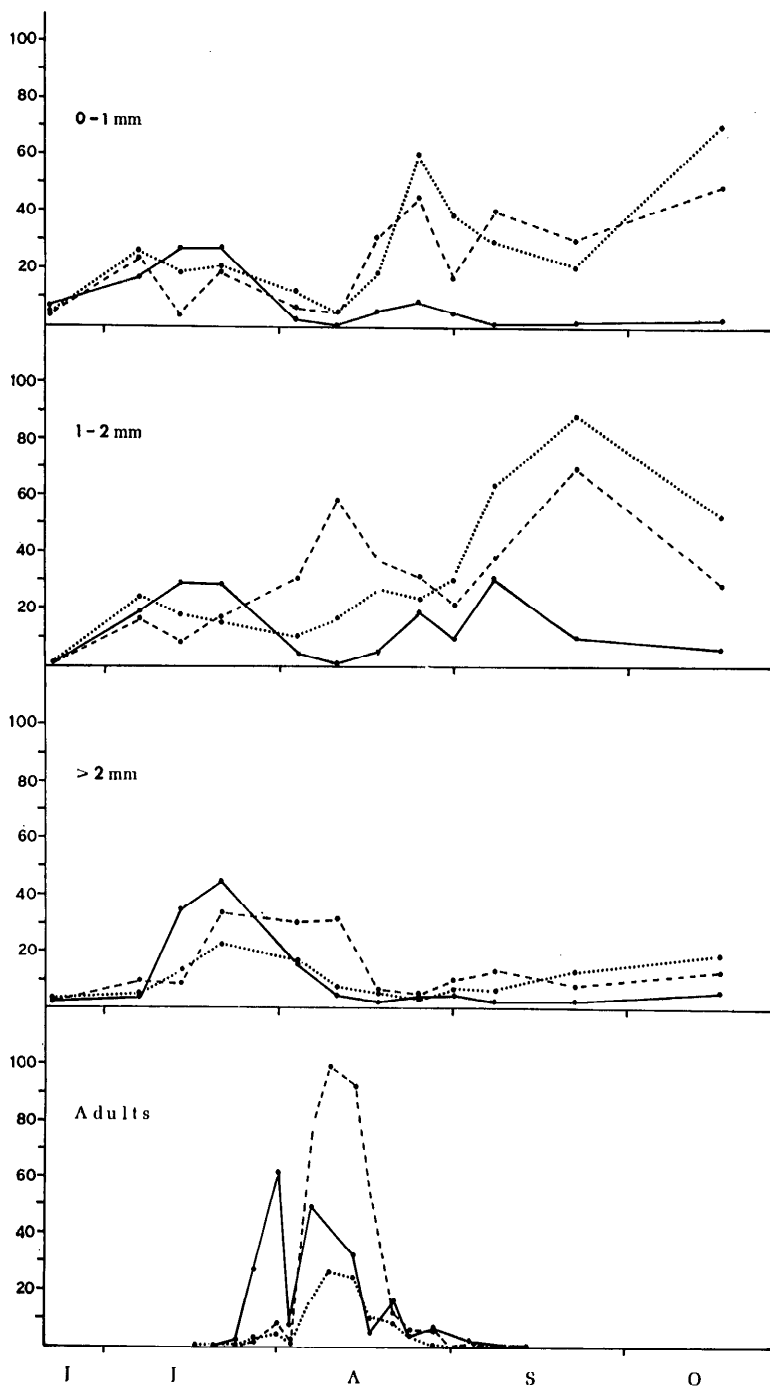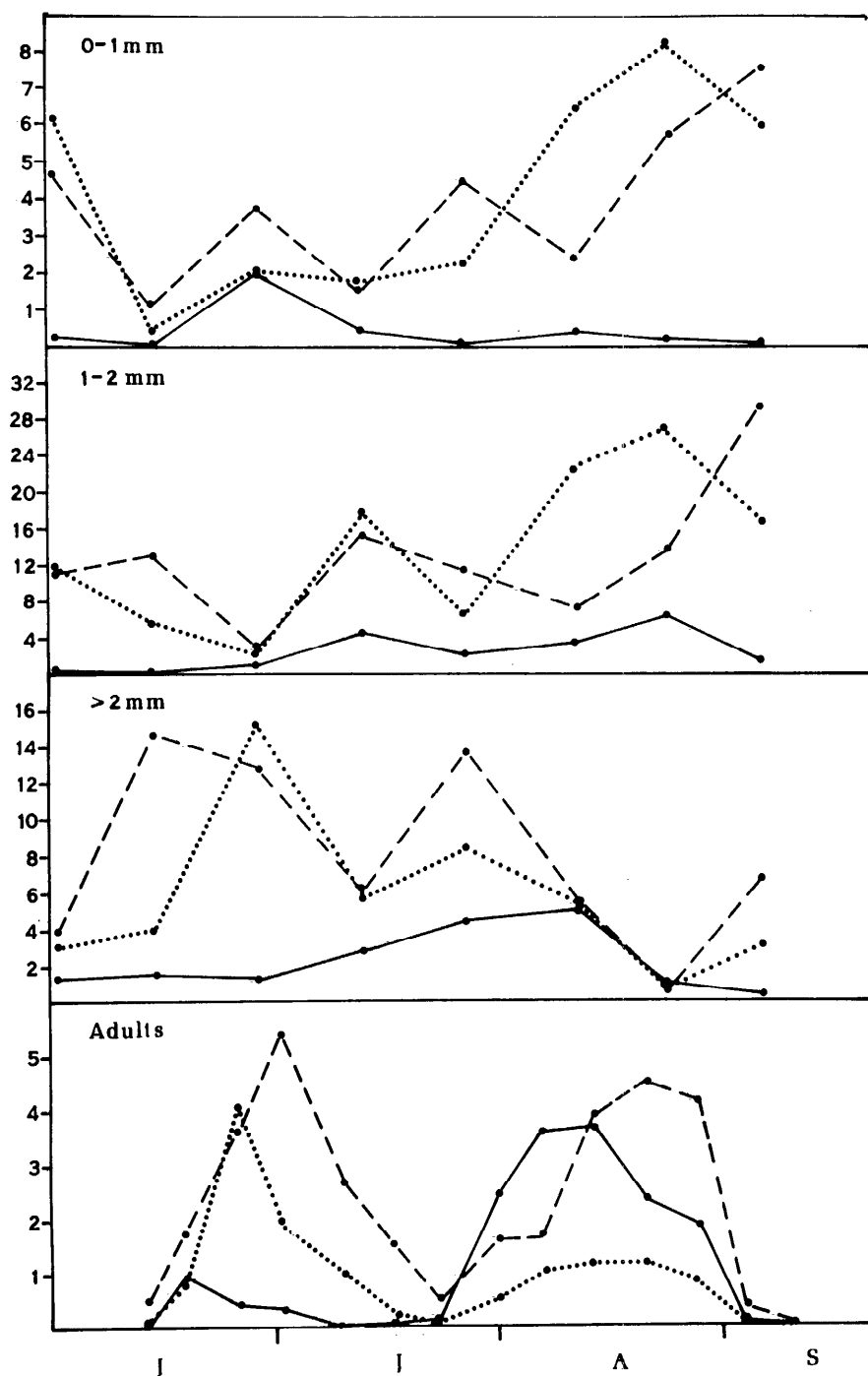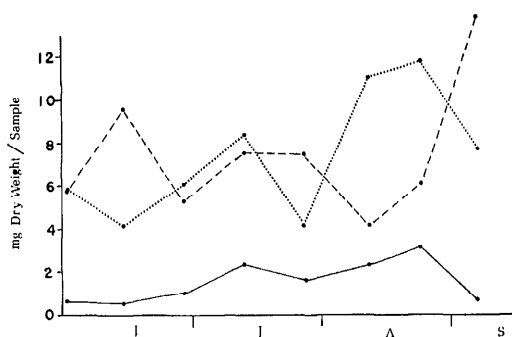
FIG. 53. Mean biomass per sample of *Caenis simulans* at three nutrient levels in 1966 (IIN ———, MN – – –, LN · · ·). Average standard errors are 2.2, 3.0, and 0.9 mg in LN, MN, and HN ponds.

then increased again. In LN and MN ponds, the standing crop was more uniform through 1966.

In mid-July 1965, the mayfly *C. simulans* increased at all three nutrient levels. These were newly recruited animals less than 1 mm long, which could be followed easily through the larger size categories (Fig. 51). The large nymphs disappeared in early August, about 30 days after the initial pulse. This reduction coincided with increased emergence rates. A second cohort of small nymphs then appeared in mid-August, undoubtedly originating from the reproductive activity of these adults (highest densities in LN and MN ponds). The populations overwintered in the small size classes. There were also two generations, with emergences in June and August, in 1966 (Fig. 52). The duration of the summer generation (late June to early August) was about 35 days. The second generation, prolonged by cold temperatures, extended from August to June. This pattern characterized all 20 ponds for the 3 years of the study; highest abundances always occurred at LN and MN levels.

The inverse effect of nutrient levels on the numerical response of the *Caenis* populations was only apparent during August in 1965 and occurred after the recruitment shifted size structures from large to small nymphs. The response of *Caenis* lagged behind that of *Chironomus* as a result of its discontinuous reproductive cycle.
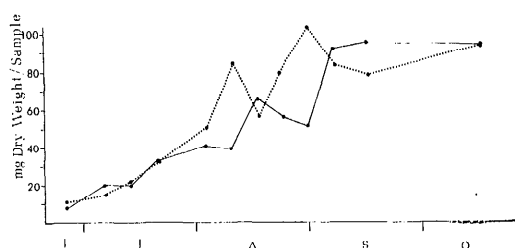
FIG. 54. Mean total benthic biomass per sample at two predation levels in 1965 (HP ———, LP · · ·). Average standard errors are 23.5 and 16.2 mg at LP and HP.

Biomass, of course, reflects the trends of the numerical data. In both 1965 and 1966 LN and MN levels supported a larger standing crop biomass of *Caenis* than did HN ponds, the reverse of the response of *Chironomus*. The peak biomass in July was contributed by large nymphs and that in September by large numbers of small nymphs. Biomass at LN and MN levels in 1966 fluctuated around 7 mg/sample until August, when there was a slight increase (Fig. 53). In the HN ponds, the biomass never exceeded 3 mg/sample. The increase in late summer occurred after emergence ceased.

Predation

The biomass of benthic organisms (excluding the large invertebrate predators) indicated little response to predation in 1965 (Fig. 54). When sampling was resumed in spring 1966, HP ponds had a 2-fold larger standing crop, which fell off

FIG. 55. Mean biomass per sample of benthic fauna at two predation levels in 1966 (IIP ———, LP · · ·). Average standard errors are 7.6 and 11.1 mg at LP and IIP.

FIG. 56.   Mean percent biomass per sample of body-size categories at two predation levels in 1965 (HP ——, LP · · ·).

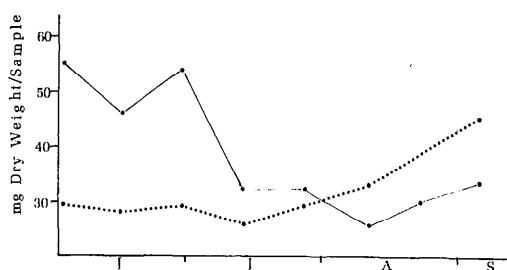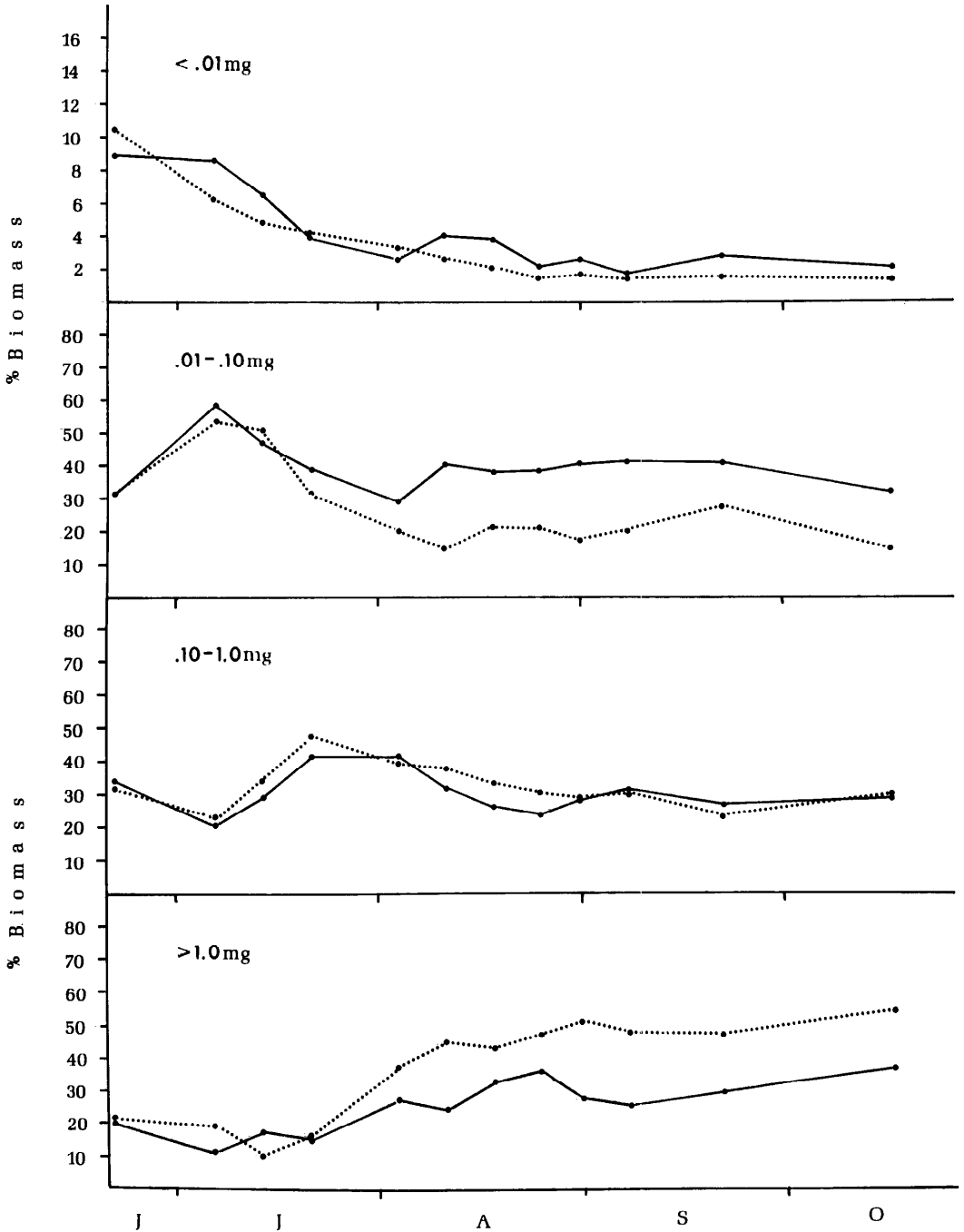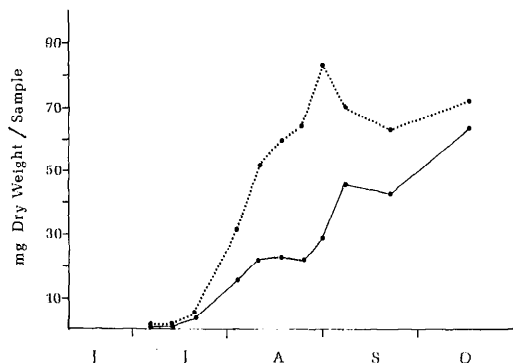FIG. 57. Mean biomass per sample of *Chironomus tentans* at two predation levels in 1965 (HP ——, LP · · ·). Average standard errors are 21.1 and 14.0 mg at LP and HP.
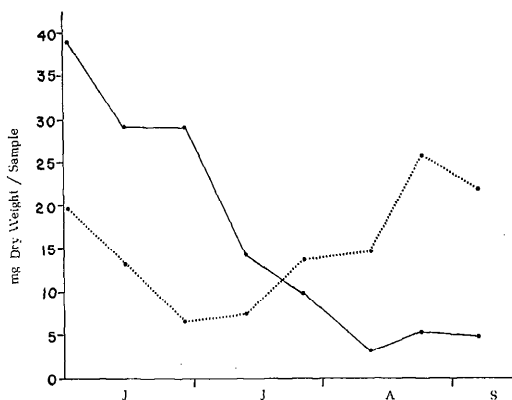
FIG. 58. Mean biomass per sample of *Chironomus tentans* at two predation levels in 1966 (HP ——, LP · · ·). Average standard errors are 5.4 and 10.5 mg at LP and HP.

rapidly. By August the trends were reversed (Fig. 55).

The effect of predation on the composition of the benthic community appears to be intimately related to the complementary responses of *Chironomus* and *Caenis*. In 1965 at LP, *Chironomus* composed about 55% of the benthos and *Caenis* 15%. But *Caenis* dominated at HP, contributing about 35% of the standing crop. In 1966 *Caenis* populations were again largest at HP, primarily in early June and late August; *Chironomus* increased only at LP in August. This relationship is also evidenced by the body size analysis. In 1965, predation increased the percent composition of small organisms (Fig. 56). The most consistent differences appeared in the 0.01–0.10-mg size range, with average compositions of 40% in HP ponds and about 20% under LP. The size category 0.10–1.0 mg remained constant, composing about 30% of the biomass of the benthos. Animals >1.0 mg contributed about 50% in LP ponds and 30% in HP ponds. These differences were apparent by mid-July and remained constant during summer. A similar pattern was found in 1966, although the differences were not as large. In early June, 70% of the benthic standing crop biomass in LP ponds consisted of the smaller two size categories. In HP ponds this was about 60%; by 6 September, 72% of the

benthos was small organisms (<0.10 mg) at LP and 86% at HP.

Since *Chironomus* and *Caenis* dominated the benthic community, little is added by other species population analysis.

Chironomus biomass was reduced when subjected to increased predation in 1965 (Fig. 57), with maximum differences in mid-August when temperatures and presumably predation rates were maximum. The effect was less by October. In 1966, biomass declined sharply in HP ponds until mid-August and remained consistently low thereafter (Fig. 58). In LP ponds, the initial reduction in biomass was associated with the period of emergences in June. Biomass increased from July through Sep-

FIG. 59. Mean biomass per sample of first instar *Chironomus tentans* at two predation levels in MN ponds in 1965 (HP ——, LP · · ·).

FIG. 60. Mean biomass per sample of third instar *Chironomus tentans* at two predation levels in MN ponds in 1965 (HP ——, LP · · ·).
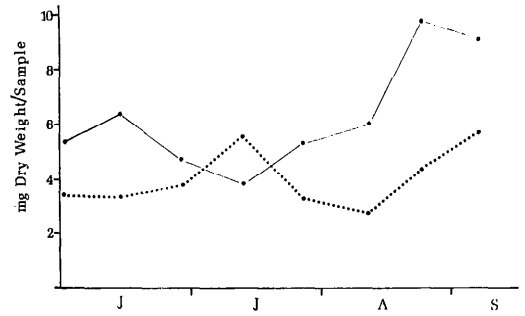
FIG. 62. Mean biomass per sample of *Caenis simulans* at two predation levels in 1966 (HP ——, LP · · ·). Average standard errors are 1.7 and 2.2 mg at LP and HP.

tember—a pattern most obvious under HN conditions.

As the body size analysis intimated, the invertebrate predation on *Chironomus* was most effective in the later instars. The first two instars were not affected (Fig. 59). The third instar under the same conditions clearly demonstrated the influence of predation (Fig. 60), as did the fourth instar. Except for the first, all instars have the same coloration, live in tubes in the sediment, and show the same kind of feeding activity. The predation effect seems to be largely a function of prey size.

The change in biomass is a product of two interacting variables: the concentration of individuals and their growth during the sample interval. With these autocorrelated data, differences in biomass accumulation are inflated through time. Third instar larvae consumed by predators cannot

contribute to the observed biomass of fourth instars at a later time, so this may account in part for the consistency in the trends with respect to predation. As the temperatures decrease in September and October, predation is reduced and the body-growth component predominates the population response, tending to reduce the difference between predation levels.

Increased predation in 1965 appeared to enhance the standing crop of *Caenis* following the August emergence (Fig. 61). In 1966, *Caenis* again increased in the HP ponds primarily in late summer (Fig. 62). The summer generation showed no difference.

Interaction of nutrients and predation

The interaction of nutrients and predation is expressed as percent difference between HP and LP, $(HP - LP)100/$
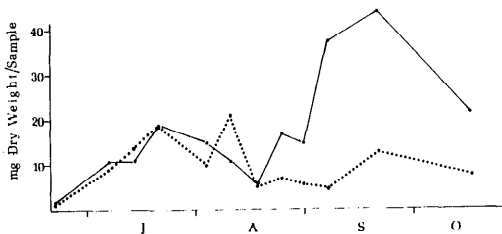
FIG. 61. Mean biomass per sample of *Caenis simulans* at two predation levels in 1965 (HP ——, LP · · ·). Average standard errors are 6.1 and 8.3 mg at LP and HP.
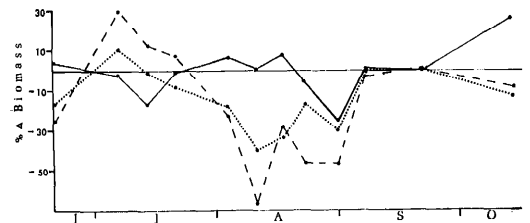
FIG. 63. Mean percent difference of total benthic biomass between HP and LP ponds at three nutrient levels in 1965 (HN ——, MN – – –, LN · · ·).
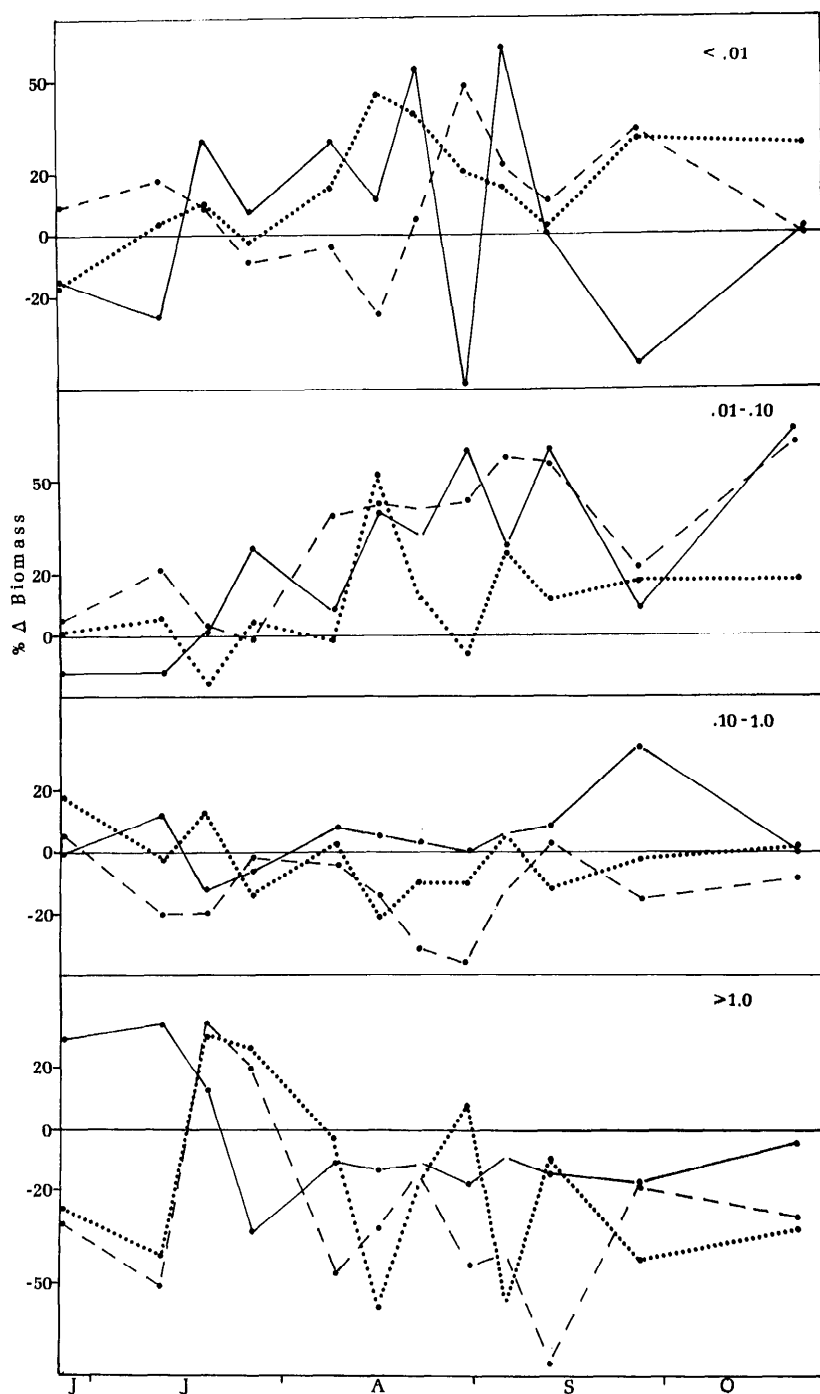
FIG. 64. Mean percent difference of benthic biomass (classified by individual body sizes) between HP and LP ponds at three nutrient levels in 1965 (HN ———, MN – – –, LN · · ·).
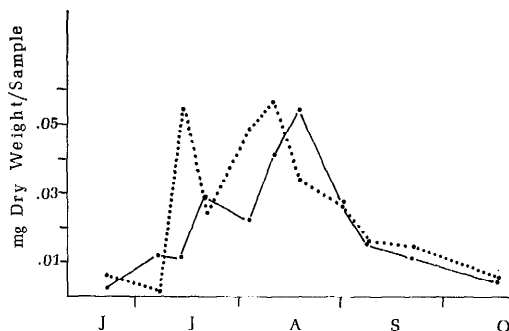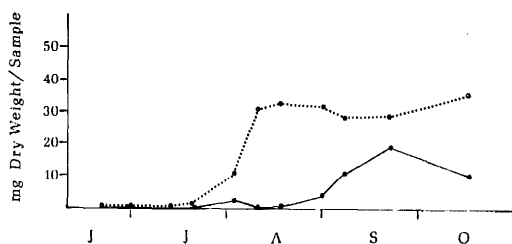
FIG. 65. Mean biomass per sample of *Chironomus tentans* at two predation levels in LN ponds in 1965 (HP ———, LP · · ·). Average standard errors are 28.6 and 2.4 mg at LP and HP.

(HP + LP), at each of the three nutrient conditions. Negative values then indicate a smaller standing crop under increased predator densities; positive values indicate higher standing crops under increased predation.

We found negative values in 1965 at LN and MN levels during August (Fig. 63). The effects of our manipulations on the total standing crop of benthos were less apparent for predation levels than for nutrient levels. In 1966, the LN and MN ponds showed no predation effect, but the trend in HN ponds indicated a shift from positive to negative values as summer progressed.
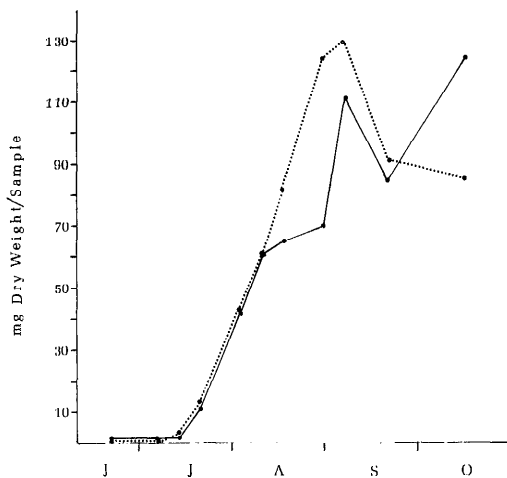
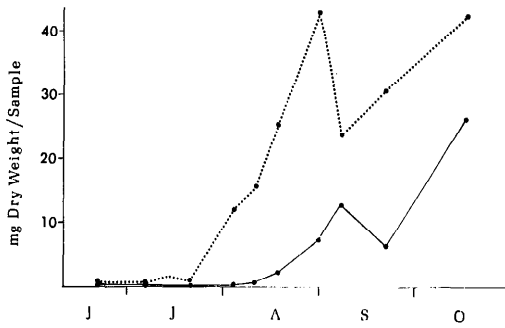
FIG. 66. Mean biomass per sample of *Chironomus tentans* at two predation levels in HN ponds in 1965 (HP ———, LP · · ·). Average standard errors are 45.0 and 24.3 mg at LP and HP.
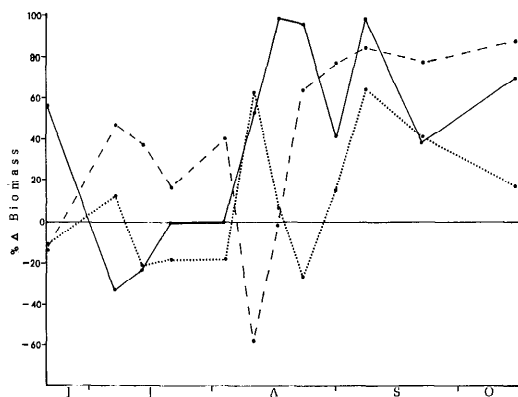
FIG. 67. Mean percent difference of *Caenis simulans* biomass between HP and LP ponds at three nutrient levels in 1965 (HN ———, MN – – –, LN · · ·).

The interaction terms demonstrated the effects of predation in a clearer fashion when we included body size. In 1965, predators selected large particles and generated compensatory increases in small prey organisms at all three nutrient levels (Fig. 64), with similar responses in 1966. The largest compensatory increase of small prey occurred in LN and MN ponds. The values for organisms >0.10 mg shifted from positive to negative during summer, with the largest differences in MN and HN ponds.

The analysis of *Chironomus* populations indicates a possible interaction of food and predation. Predators at LN reduced the biomass of *Chironomus* in 1965 (Fig. 65). At MN the same pattern is apparent, but the differences are greater. At HN the predation effect is essentially eliminated (Fig. 66) despite the fact that the emergence of *A. junius*, which were feeding primarily on third and fourth instar *Chironomus* (Ross 1967), was 2.5 times greater in HP ponds. This absence of an effect at HN may be due to an increased turnover rate of the prey population, to a reduction in the relative effect of predation on the increased biomass, or both. Laboratory experiments demonstrated an inverse relationship between food level and instar duration (Fig. 35); field data (Fig. 48)

also indicate a time lag in larval response inversely related to nutrient levels. Both suggest the possibility of increased turnover at higher nutrient levels.

At all three nutrient levels in 1965, *Caenis* biomass indicated a positive response to predation level (Fig. 67), with the greatest effects at LN and MN. In 1966 the same effect in late summer was evident at LN and MN but not at HN. These populations seemed to respond negatively to increasing nutrient concentrations so that the most striking predation effects were observed at the lower nutrient levels.

Production

Our production estimates are based on two different models. Populations with synchronous and discrete reproductive periods are characterized by age structures that progress from young to old organisms in a wavelike fashion. At any given time, most of the animals will be of the same instar. Production can be estimated in such a population by combining numerical abundance with body size; we have done this for *Caenis*.

The procedure for estimating production of *Chironomus* is more complicated. Recruitment is continuous and the population usually includes all four instars, so standing crop estimates do not provide an adequate measure of production. These populations are turning over at various rates as a function of nutrients, predation, and season of the year. Production is estimated by the extrapolation of the observed population over brief time intervals (Cooper 1965). At each time, the difference between the observed and the expected numerical abundance of each instar is a measure of mortality. Production is estimated by the sum of mortality, emergence, and net increase in standing crop biomass.

Caenis simulans. Data from 1965 and 1966 indicate two generations per year with emergence and reproduction occurring over 1-month periods. The development of the summer generation takes about 6 weeks (Fig. 52). It cannot be assumed that changes in biomass represent only mortality

TABLE 18. Caenis simulans *production estimates (mg dry wt/232 cm²) from 20 July to 16 October 1965*

	$\bar{x} \pm$ SE
Nutrient level	
HN	4.2 ± 11.2
MN	23.2 ± 11.2
LN	33.2 ± 9.7
Predation level	
HP	32.4 ± 9.1
LP	10.3 ± 9.1
Nutrient × predation	
HNHP	6.3 ± 15.8
HNLP	2.0 ± 15.8
MNHP	42.0 ± 15.8
MNLP	4.3 ± 15.8
LNHP	49.0 ± 15.8
LNLP	24.7 ± 15.8

and individual body growth because recruitment occurs during two-thirds of the life of the summer generation. Our production estimates for *Caenis* did not include this turnover, so they are minimal.

Production was estimated as the sum of standing crops of *Caenis* nymphs on sampling dates just before emergence. Only the portion of individual body growth after 21 June 1965 was included from the overwintering cycle. Average standing crop biomass between 21 September and 16 October 1965, when recruitment and individual body growth were negligible, was used as the production estimate for the second generation.

Caenis production was highest in LN and MN ponds (Table 18). There was a trend toward increased production under HP, but the standard errors are too large to permit statements of significant differences. A strong block effect increased the variances in production estimates; average production of *Caenis* for the three blocks of ponds was 38.2, 16.0, and 77.8 mg/232 cm².

The within-treatment variance is reduced when the production estimates are divided into their temporal components. The summer generation was entirely under the influence of our manipulation and reflected the effect of predation and nutrients more

TABLE 19. *Extrapolation procedure for Chironomus tentans production estimates*

Days duration of stage at 23C		Observed numerical density at time x
Instar		Instar
1st:	$t_1 = 3$	1st $= n_1$
2nd:	$t_2 = 4$	2nd $= n_2$
3rd:	$t_3 = 9$	3rd $= n_3$
4th:	$t_4 = 13$	4th $= n_4$
Pupae:	$t_p = 3$	Pupae $= n_5$

Duration of the sample interval $= t_s$
Assume a constant recruitment rate of n_1/t_1 over the period t_s

Estimated number of animals at time $x + t_s$
Instar: 1st $= n_1$
2nd $= (n_1/t_1)t_2$
3rd $= n_1 + n_2 + (1 - t_s/t_3)n_3$
    if $t_3 < t_s$, then $(1 - t_s/t_3) = 0$
4th $= n_3(t_s/t_3) + n_4(1 - t_s/t_4)$
    if $t_3 < t_s$, then $t_s/t_3 = 1$
    if $t_4 < t_s$, then $(1 - t_s/t_4) = 0$
Pupae $= n_4(t_s/t_4)(t_5/t_s)$
Emergent $= n_4(t_s/t_4)(1 - t_5/t_s)$

TABLE 20. *Production estimates for Chironomus tentans*

$\bar{x}$ numbers (3 August)		$\bar{x}$ numbers (10 August)		$\bar{x}$ numbers (3–10 August)	
Stage	Obs.	Ex-pected	Obs.	Stage	Difference (obs. − expected)
1st	33.3	33.3	83.0	1st	+49.7
2nd	84.0	44.4	61.3	2nd	+16.9
3rd	34.3	125.0	28.0	3rd	−97.0
4th	14.3	33.3	17.3	4th	−16.0
Pupae	0	3.3	0	Pupae	−3.3

Estimated number of adults $= 4.4$
Increase in standing crop $= 0.39$ mg
Estimated mortality $= 70.43$ mg
Emergence $= 4.64$ mg
Total production $= 75.46$ mg

distinctly than the spring component. Average production in IIN ponds was 22.1 mg for the spring and 4.2 mg for the summer generations. In IIN ponds, *Caenis* completed the preexisting generation but did not establish a productive summer generation.

Production estimates for *Caenis* in 1966 are the summation of standing crops at three times during summer. One component consists of the average difference in biomass between 1 and 28 June, that is, just before the early summer emergence (Fig. 52). The second component is the average standing crop biomass of the pond on 26 July, representing the maximum standing crop of nymphs before the August emergence. The temporal sequences of these patterns vary between ponds, but no systematic trends appear to bias the estimates as a function of manipulations. The third component of *Caenis* production is the increase in biomass of nymphs between 1 August and 6 September, which will emerge in June 1967. Relative contributions of the three components to *Caenis* production overall averaged 31.6% for early summer growth, 25.1% for the midsummer

generation, and 43.1% for late summer growth. Estimates based on these three components are minimal production values.

The effect of nutrient and predation levels on 1966 production resembles that in 1965. HN levels inhibited *Caenis* production. The average production estimates are 19.1, 27.1, and 4.8 mg per sample area in LN, MN, and HN ponds.

Chironomus tentans. An example of the procedure used for estimating production when populations have overlapping generations follows. On 3 August 1965 an average of 33.3 first instar *Chironomus* per sample was collected from pond 38. The duration of first instar larvae at 23C is 3 days (Table 19). Assuming constant recruitment during the 7-day interval between samples (33.3/3), 11.1 first instar animals will be added to the population per day (Table 20). New estimates of recruitment are available at each sample date. The expected number of first instar animals is the recruitment rate, 11.1/day, times the duration of the first instar, 3 days. On 10 August the expected number is $11.1 \times 3 = 33.3$ first instar animals.

The estimated number of second instar *Chironomus* is the recruitment rate of 11.1 animals/day times the duration of the second instar, 4 days, or 44.4 animals/sample. For a sample interval of 7 days, all of the first or second instar animals observed on 3 August will reach, but none will grow

beyond, the third instar. The expected number of third instars on 10 August is then the sum of the first two instars observed on 3 August plus a proportion, $(1 - t_8/t_3)$, of the observed third instars that did not have enough time to reach the fourth instar. In the example, the expected number is $33.3 + 84.0 + (2/9) 34.3 = 125.0$ animals.

The estimated number of fourth instars has a complement of animals that were third instars the preceding week, plus those animals that failed to develop out of the fourth instar in the 7-day period. The fourth instar recruitment is $(7/9) 34.3 = 26.7$ individuals. The number of fourth instar *Chironomus* expected on 3 August to remain in this instar until 10 August is $(1 - 7/13) 14.3 = 6.6$. The expected number of fourth instars on 10 August is $6.6 + 26.7 = 33.3$. The same procedure is used to estimate the expected number of pupae and emergent adults.

Summation of the observed densities minus those expected for each instar over the summer (Table 21) provides an estimate of the net difference or total estimated mortality in the larval population. Positive values indicate an underestimation in the density projection—a kind of error probably due to differential developmental rates in the different ponds and to errors in estimating the previous instar category. Density of the second instar was generally underestimated, especially in the more productive ponds. This is probably related to the assumption of constant recruitment at the rate of n_1/t_1. Density estimates of the first instars (n_1) are the least accurate because of errors in identification and losses during sampling and extraction.

Relative durations of the instars were determined from both field data (Fig. 48) and growth experiments at 23C (Fig. 35). Apparent generation time, that is, the period between the initial response in first instar *Chironomus* to increased nutrients and the first pulse in emergent adults (Fig. 48), was about 32 days. All adult *C. tentans* collected in the emergence traps were large, indicating moderate to high levels of

TABLE 21. *Number observed minus number expected (21 June to 7 September 1965)*

Pond	Instar categories of *Chironomus tentans*				
	1st	2nd	3rd	4th	Pupae
Block I					
22 LN	0.3	71.7	−14.9	−6.5	−0.6
26 LN	−0.3	−0.8	−38.3	−6.1	−1.5
21 MN	4.0	23.2	−17.8	−7.8	−0.62
25 MN	3.7	217.9	3.7	−225.9	−39.1
23 HN	7.7	47.5	2.8	−46.4	−22.1
24 HN	−0.3	30.1	125.5	−166.0	−40.8
Block II					
30 LN	3.0	0.9	−16.0	−4.0	0.0
31 LN	4.0	1.8	−8.7	−0.3	0.0
29 MN	2.6	−11.9	−43.4	0.1	−0.1
28 MN	3.2	8.0	−11.63	0.5	−0.2
32 HN	−0.4	307.2	−146.4	−152.5	−10.3
33 HN	0.26	190.1	41.7	−87.3	−14.0
Block III					
37 LN	1.0	100.98	146.13	−133.9	−40.6
40 LN	1.76	4.8	−111.1	−9.0	−0.1
36 MN	0.7	168.6	120.8	−122.9	−53.7
39 MN	0.7	84.6	−183.5	−38.2	−4.7
35 HN	−1.3	127.1	240.7	−20.1	−93.9
38 HN	8.4	268.4	−426.1	−116.6	−25.1
Control					
27 CN	2.7	34.2	−60.9	−8.3	−0.5
34 CN	6.3	80.2	−294.5	−33.4	−0.8

food. The generation time was partitioned into the five aquatic stages using laboratory data at comparable food levels (Fig. 35).

Variations in estimates of population size and structure are a function of the density and distribution of the animals; they change with both time and experimental manipulation and will affect the differences between observed and expected populations. Over the summer, this type of random error within instar categories should cancel out since both positive and negative deviations are integrated and all estimates are summed over the growing period.

The assumption of constant recruitment is not critical to estimates of biomass production since the only errors associated with it involve the early instars $(t_s \leqslant 14$ days), which are small and do not contribute significantly. The production model treats recruitment into each instar as a function of previous instar abundance and

TABLE 22. Chironomus tentans *production estimates (mg dry wt/232 cm²) from 21 June to 7 September 1965*

	$\bar{x} \pm$ SE
Nutrient level	
HN	381.0 ± 54.6
MN	194.5 ± 54.6
LN	99.6 ± 47.4
Predation level	
HP	171.4 ± 44.6
LP	271.0 ± 44.6
Nutrient × predation	
HNHP	402.0 ± 77.3
HNLP	360.0 ± 77.3
MNHP	72.0 ± 77.3
MNLP	317.0 ± 77.3
LNHP	40.3 ± 77.3
LNLP	136.0 ± 77.3

TABLE 23. Chironomus tentans *production from 1 June to 6 September 1966 (mg dry wt/232 cm²)*

	Change in biomass	Mortality	Emergence Predicted	Emergence Obs.
HN	−23.53	+27.48	+99.49	18.55
MN	−12.31	+61.70	+42.56	8.03
LN	−6.81	+91.79	+28.22	3.90
HP	−33.85	+29.12	+70.59	8.19
LP	+2.06	+85.49	+40.71	11.69
HNHP	−75.82	−43.14	+166.70	18.94
IINLP	+28.76	+98.10	+32.27	18.16
MNHP	−6.62	+30.67	+21.09	3.08
MNLP	−21.33	+92.71	+64.02	12.99
LNHP	−19.10	+99.83	+10.42	2.55
LNLP	−4.14	+65.63	+24.42	3.91
Control	+7.62	+118.95	+40.26	5.93

developmental rates, so errors in estimating first instar abundance are not amplified appreciably during the relatively short (7 day) production interval. Estimates of size-specific mortality, based on weekly differences between observed and expected populations, assume that these average differences will differ from zero only when mortality factors operate consistently during summer.

The methods of estimating mortality are critical because the biomass estimated to have been removed by mortality is 65.5% ± 5.0 ($\bar{x} \pm$ SE) of the total population for all 20 ponds. The bias introduced by underestimating second instar animals and by using generation times associated with moderately productive conditions will make these estimates conservative.

These production estimates for *Chironomus* have three components. An estimate of standing crop each week records changes in population size. The other two components represent turnover within populations, consisting of the biomass lost by larval mortality and emerging adults.

All of the emergence estimated does not actually occur, since the model assumes no pupal mortality, but it is still *bona fide* production. In 1965, the average percent contributions of these three components to total production were ($\bar{x} \pm$ SE): increased

standing crop = 26.6 ± 4.3%, mortality = 65.5 ± 5.0%, emergence = 7.9 ± 1.9%.

The total production estimated for *Chironomus* in 1965 (Table 22) indicates a significant ($P = 0.02$) 3.8-fold increase in the HN ponds over LN and a 1.5-fold increase in LP over HP ponds. The interaction of nutrient and predation levels indicates that predation was most effective in reducing production at the LN and MN levels, in agreement with our biomass data. Neither the predation effect nor the interaction of nutrient and predation is statistically significant.

Production for *Chironomus* in 1966 was estimated from a slightly modified version of the above model, with two basic changes. First, the data in 1966 are based on 2-week sampling intervals. The second change concerns the general decline of *Chironomus* populations in 1966. The standing crops in spring 1966 were high as a result of the 1965 response to nutrient addition, but 15 of the 20 populations showed a net loss during summer 1966, with populations in HN ponds having the greatest decline. Pond 25, MN and LP, is the only pond with any appreciable increase in *Chironomus*. Production in 1966, then, is simply the sum of mortality and emergence rates estimated from the model. The mortality component averaged 63.75 ± 5.6% of the total *Chironomus* production. The production components indicate a strong predation effect in HN ponds in 1966 (Table 23).

TABLE 24. Chironomus tentans *production from 1 June to 6 September 1966 (mg dry wt/232 cm²)*

		Nutrient level		
	Block	LN	MN	HN
Predation level				
LP	I	82.70	188.89	87.52
	II	8.33	46.45	21.17
	III	179.14	234.79	282.46
HP	I	102.73	60.55	102.93
	II	102.96	13.84	127.35
	III	165.73	80.91	140.40
Average		106.93	104.24	126.97
Control				
Pond 27	120.88			
Pond 34	197.46			

FIG. 68. Mean biomass per sample of benthic fauna at three nutrient levels in 1967 (HN ———, MN – – –, LN · · ·). Average standard errors are 5.7, 8.5, and 11.1 mg in LN, MN, and HN ponds.

These relationships are a function of the instar distributions of the larval populations and of the reduction in population size. The instar distribution was skewed toward terminal instars, resulting in high values for expected emergence in ponds with large overwintering populations. These ponds were primarily at HN levels and they also showed the greatest net decrease in 1966.

Mean production of *Chironomus* per pond for 1 June–6 September, expressed as mg dry wt/sample area, showed no significant effects of nutrient level (Table 24).

There is a significant block effect ($P < 0.01$) with a pattern similar to that observed in 1965. Average production per sample area was 180.57 mg in block III, 53.35 mg in block II, and 104.22 mg in block I. The block × nutrient interaction sum of squares is small, indicating no interaction.

Average production for *Chironomus* did not differ at the two predation levels. Production averaged 125.72 mg in LP ponds and 99.71 mg in HP ponds. In general, there was no effect from any manipulations on *Chironomus* production in 1966.

Results 1967

Nutrients

Total biomass. Total benthic biomass in early spring was positively related to nutrient level (Fig. 68). There was a steep reduction in average standing crop as water temperatures increased, most likely because of increased emergence rates and fish predation. The decrease was greatest in HN ponds which declined from 64 mg/sample in April to about 25 in August (about the level of LN ponds). This decline was also associated with the development of macrophyte populations. The biomass at MN levels increased during the postemergence period to 1965 levels (about twice those of 1966); this is not surprising as the fertilization rate at MN was raised from 0.23 to 0.69 kg/week in 1967. The LN ponds increased consistently all summer, from 15 to 35 mg—comparable with values in 1965 and 1966.

The cumulative weight of emergent insects per trap-day is given in Fig. 69. The step increase in early summer at HN levels represents the large overwintering population of late instar *Chironomus*. Emergence rates after mid-July were consistently low and not related to nutrient levels.

Community response. The percentage of the total biomass of the benthos contributed by *Chironomus* in early summer 1967 averaged 12% in LN, 49% in MN, and 60% in HN ponds (Fig. 70), indicating different rates of accumulation for the *Chironomus* populations between September 1966 and April 1967. The composition in September 1966 was about 20% in MN and LN ponds
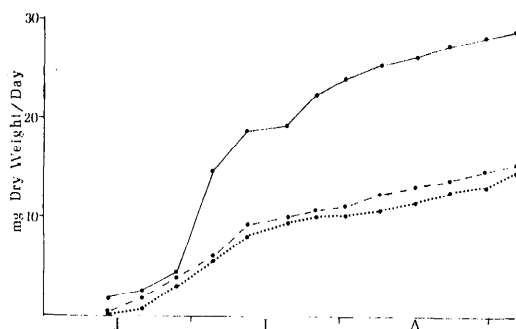
FIG. 69. Cumulative weekly estimates of emergence rates expressed as mg dry wt trap^{-1} day^{-1} at three nutrient levels in 1967 (HN ——, MN – – –, LN · · ·).

and 30% at HN levels. *Chironomus* declined slowly but consistently through summer in the MN and HN ponds. At LN, the relative amount of *Chironomus* increased in July and then declined uniformly to approximately the spring values.

Caenis was less than 5% of the benthos at all nutrient levels until July. It then increased in both LN and MN ponds to over 25% of the benthic standing crop; this did not occur in the HN ponds. *Caenis* also increased in late summer the 2 years previous.

Standing crops of Zygoptera were of major importance for the first time in 1967 (Fig. 70). Their relative contribution was greatest in early spring and inversely proportional to nutrient level. These were populations of late instars at relatively low densities. The June emergence replaced this biomass with a large number of small instars.

The "others" category consisted of a large number of taxa, none of which contributed more than 10% of the biomass. This collection of nonabundant taxa contributed from 40 to 60% of the biomass and was quite uniform throughout summer 1967.

Body size. The distribution of biomass in the body-size categories was similar to that in 1966. In LN and MN ponds about 90% of the biomass consisted of animals <0.10 mg dry wt. The larger categories contributed slightly more in spring and fall,
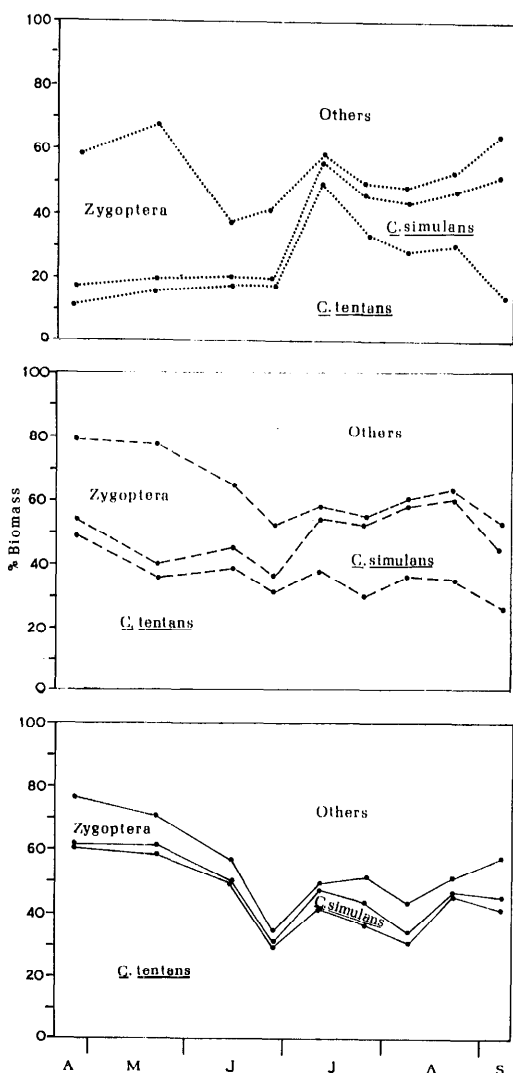
FIG. 70. Mean percent biomass per sample of benthic fauna at three nutrient levels in 1967 (HN ——, MN – – –, LN · · ·).

but were never a dominant component. On the other hand, in HN ponds 55% of the biomass in April consisted of large organisms >0.10 mg. These declined to about 15% in July and then increased again to 35% by September The larger sizes were not nearly as dominant at HN as in previous years.

Size-frequency distribution. Frequency distributions of small animals (<0.01 mg) in the samples in 1967 were similar to

those in 1965 and 1966 (Fig. 46). LN and MN levels were similar; under HN conditions, the distribution was skewed toward lower numbers. The picture for large animals (>1.0 mg) was almost identical with that of 1965 (Fig. 47). The frequency of low density samples seemed inversely related to nutrient level.

Population responses. The numerical response of *Chironomus* in 1967 produced a third pattern of population development (Fig. 71). In April, the populations were composed of third and fourth larval instars and pupae. The effect of nutrient application the previous year was again evident in the densities of overwintering stages, which declined during May and June as a result of high emergence rates. The last burst of emergence was recorded on 10 June and a pulse of first instar *Chironomus* was produced by mid-June. This cohort could be followed through the second instar in late June and into the third instar by early July. The nutrient effect on these early instars is inconclusive. The clear, positive relationship between *Chironomus* and nutrient level observed in 1965 was not apparent in 1967.

Densities of fourth instar *Chironomus* were reduced from about 25/sample in April to <8/sample for the latter part of summer. Average densities did not show an increase in late summer as was seen in the previous 2 years.

Distributions of pupal densities and adult emergence rates indicated two periods of high emergence activity—one in May and the other in September. During summer, the rate of emergence was uniform but low at all nutrient levels. The populations were all turning over slowly with no apparent nutrient effect.

The biomass of *Chironomus* demonstrated the same trends. Biomass in HN ponds declined sharply until early August and then increased slightly. Biomass in MN ponds declined slightly in midsummer and then increased to about the level of April. The standing crop in LN ponds increased in the later part of summer.

The numerical response of *Caenis* was

Fig. 71. Mean numerical densities of life-history stages of *Chironomus tentans* at three nutrient levels in 1967 (HN ———, MN – – –, LN · · ·). Adults counted as No. trap^{-1} day^{-1}; all others as No./sample.

more difficult to interpret in 1967 than in the preceding 2 years (Fig. 72). The spring populations were composed of nymphs >1 mm long. This size distribution remained constant until late June when increasing numbers of adults were caught in the
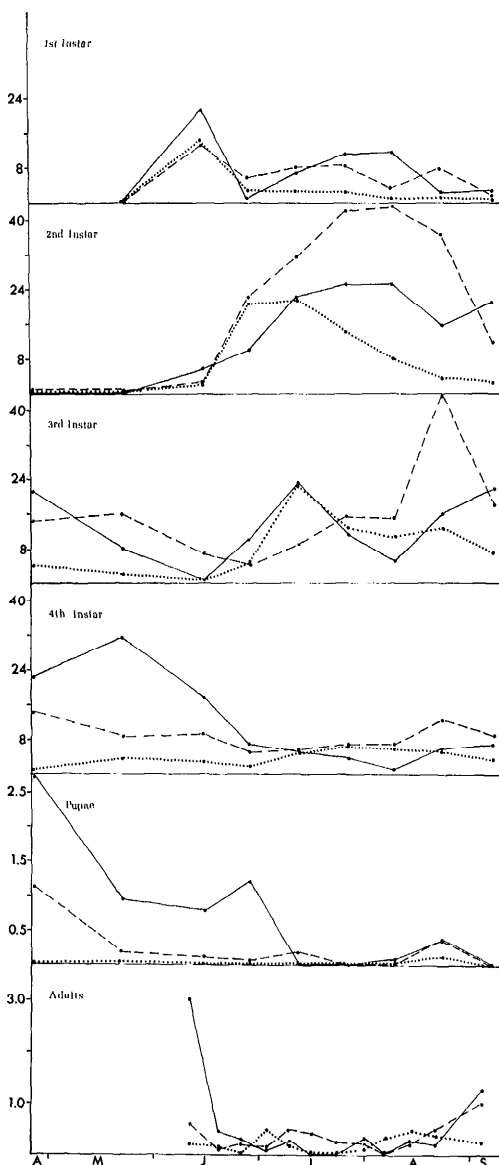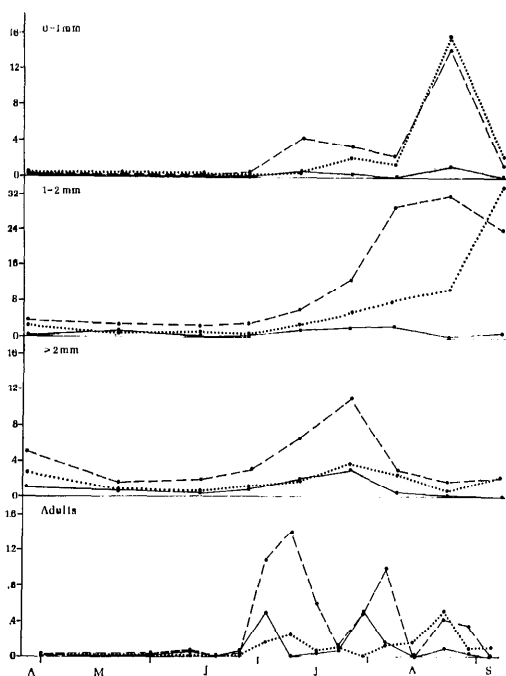
FIG. 72.   Mean densities of life-history stages of *Caenis simulans* at three nutrient levels in 1967 (HN ——, MN – – –, LN · · ·). Adults counted as No. trap^{-1} day^{-1}; all others as No./sample.

emergence traps. In early July, a cohort of small nymphs (up to 1 mm long) appeared in the MN ponds, presumably produced by the adults that emerged in late June. This cohort was followed through the increasing size categories to an emergence peak about 30 days later in early August. The period
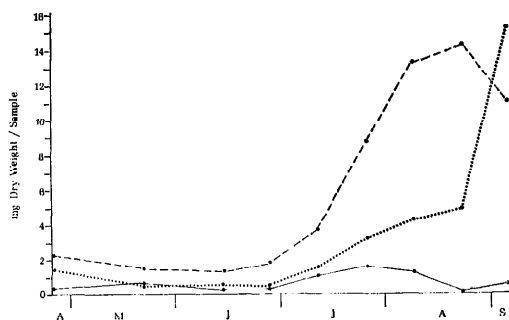
FIG. 73.   Mean biomass per sample of *Caenis simulans* at three nutrient levels in 1967 (HN ——, MN – – –, LN · · ·). Average standard errors are 1.1, 2.8, and 0.4 mg in LN, MN, and HN ponds.
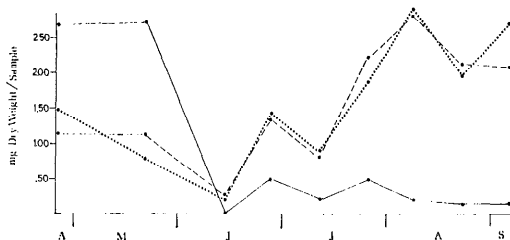
FIG. 74.   Mean biomass per sample of *Hyalella azteca* at three nutrient levels in 1967 (HN ——, MN – – –, LN · · ·).

between emergence peaks was similar to that in 1966. Late summer emergence produced a large population of small nymphs (<2 mm long) in LN and MN ponds. The fall population, consisting primarily of small mayflies, was similar to those of 1965 and 1966.

We cannot explain the low densities of small mayflies in early June preceding the midsummer emergence. There is some evidence that large nymphs moved into very shallow water before emergence, but this was not observed for young nymphs. In general, *Caenis* was not as abundant in early summer 1967 as in 1965 and 1966. The nutrient manipulations again resulted in large standing crops of *Caenis* in LN and MN ponds (Fig. 73). The increase, delayed at all nutrient levels until early July, occurred first in MN ponds.

Biomass of damselflies was maximum in mid-May before the early summer emergence. There were no clear differences with nutrient levels either in spring or fall. During July and August the nymphs were in the early instars and did not contribute more than 2 mg dry wt/sample. By late August, the biomass was again increasing.

Hyalella azteca was most abundant in April in HN ponds (Fig. 74); from June onward, the largest standing crops were observed in LN and MN ponds, which showed no differences.

Tanytarsini, a group of small midges, responded to the nutrient manipulations as did *Caenis*: Biomass increased during summer at LN and MN levels.

FIG. 75. Mean biomass per sample of benthic fauna in ponds with and without fish in 1967 (F ——, WF · · ·). Average standard errors are 7.2 and 8.2 mg in F and WF ponds.
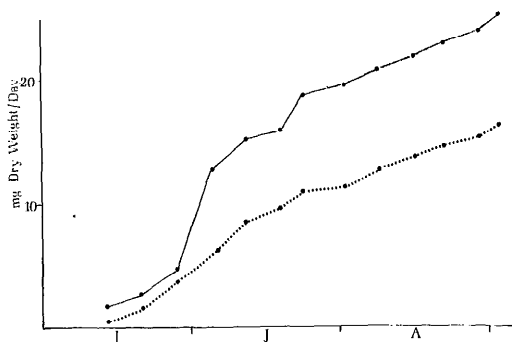
FIG. 76. Cumulative weekly estimates of emergence rates expressed as mg dry wt trap^{-1} day^{-1} at two predation levels in 1967 (F ——, WF · · ·).

Predation

Fish predation had no demonstrable effect on total benthic biomass (Fig. 75). Differences were small, brief, and easily within sampling variation. But the presence of fish had a more decisive effect on emergence rates (Fig. 76), primarily a result of the size-specific nature of the fish predation and the vulnerability of pupae. The effect of fish predation on emergence was essentially the same at all three nutrient levels.

The predation effect influences the percentage composition of only a few species of benthos. The values for *Chironomus* were almost identical in ponds with and without fish. *Caenis* in ponds with fish contributed about twice the percentage estimated for ponds without fish. This difference was apparent from early July until September. Damselflies declined in proportion in ponds with and without fish by mid-June, but more so in those with fish. The ponds without fish, however, showed an increase in damselflies in late summer as the nymphs grew into larger instars, which were entirely absent in ponds with fish. The "others" category did not reflect the effect of fish predation. Although individual taxa within this group may have been affected, their responses were masked by summation.

Fish slightly increased the relative abundance of small organisms in the benthos.

In April, larger animals (>0.10 mg) accounted for 25% of the biomass in ponds without fish and 35% in those with fish. A combination of spring emergence and predation reduced these values to about 10% by mid-June. This remained the case in ponds with fish for the rest of summer. In ponds without fish, the contribution of large items increased to about 20% by September. But the smaller organisms dominated the benthic community in all ponds.

The presence of fish did not alter the frequency distribution of densities observed in the samples for either small or large organisms. As sizes increased, the distributions were restricted to lower densities. This pattern was apparent whether the ponds did or did not have fish.

In general, three taxa responded negatively to fish predation and two responded positively. The numerical response of *Chironomus* to fish predation indicated a pattern of population development different from that shown when fish were absent (Fig. 77). Larger instars and pupae were more abundant in ponds with fish in April; by mid-June, these densities were reversed and ponds without fish had more third and fourth instar *Chironomus* for the rest of summer. This is clearly shown by the biomass of *Chironomus* (Fig. 78). In general, small instars were not affected by the presence of fish.

The number of emerging adults was also
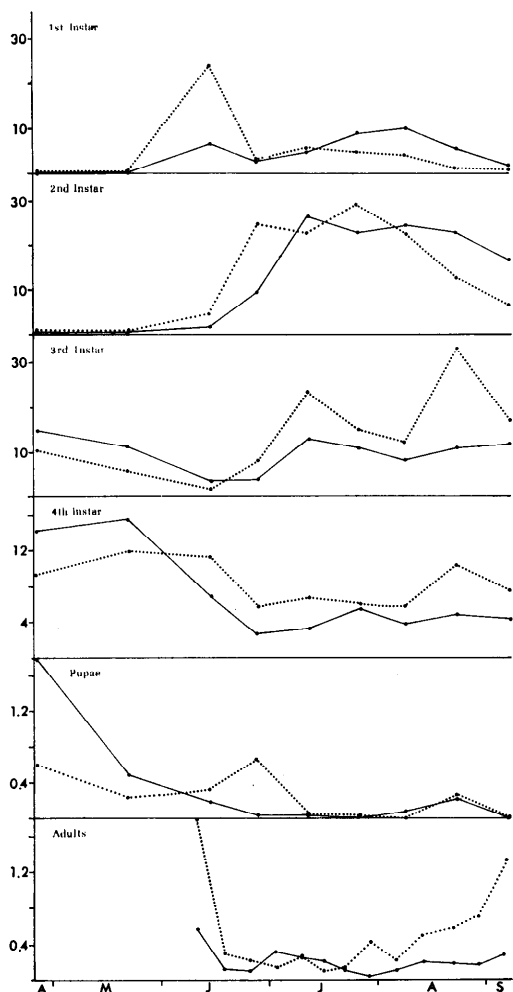
FIG. 77. Mean densities of life-history stages of *Chironomus tentans* in ponds with and without fish in 1967 (F ——, WF · · ·). Adults counted as No. trap^{-1} day^{-1}; all others as No./sample.
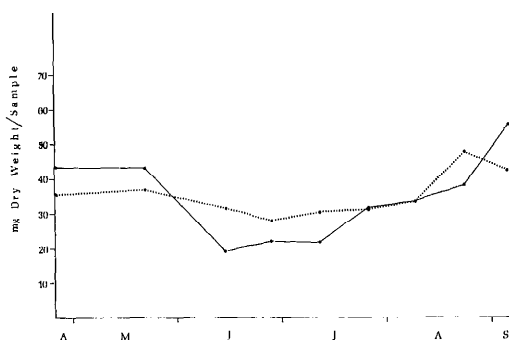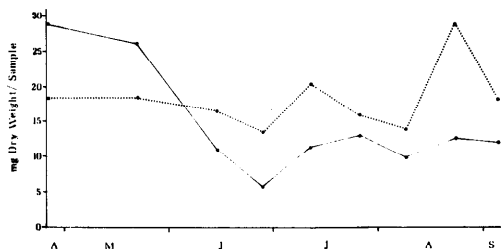

FIG. 78. Mean biomass per sample of *Chironomus tentans* in ponds with and without fish in 1967 (F ——, WF · · ·). Average standard errors are 6.7 and 5.2 mg in F and WF ponds.
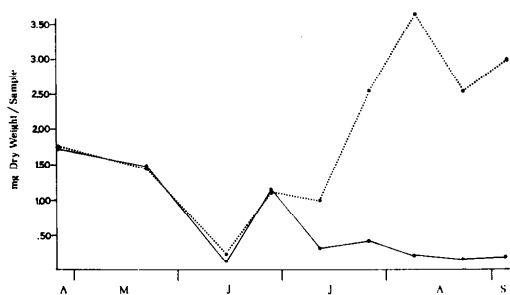

FIG. 79. Mean biomass per sample of *Hyalella azteca* in ponds with and without fish in 1967 (F ——, WF · · ·).

greater in ponds without fish during the two periods of high emergence. In mid-summer when densities of pupae and adults were low, no fish effect could be detected. The bimodal emergence pattern was therefore more obvious in ponds without fish than in those with fish.

The biomass of Zygoptera was lower in ponds with fish. A general spring decline in biomass was followed by a late summer increase only in ponds without fish—an effect evident at each nutrient level. *Hyalella* (Fig. 79) showed no effect until July when populations in ponds without fish began increasing rapidly. The populations in ponds with fish declined through August.

Caenis increased most rapidly in LN and MN ponds with fish, beginning in late June and continuing at a constant rate through early September. In ponds without fish the increase was inhibited during July and August. Tanytarsini responded similarly to fish predation, particularly in July and August, with the greatest effect at MN levels.

Production

The production of *Chironomus* in 1967 was estimated as the sum of the standing crops at three dates during summer (27 June, 25 July, and 7 September), following the procedure for 1966. The bimodal emergence pattern was again apparent (Fig. 72) though less pronounced than in 1965 and 1966. The three components contributed 5.4, 29.6, and 64.9% of the total production. The average production estimates are given

TABLE 25. Caenis simulans *production (mg dry wt/232 cm²) from 9 June to 7 September 1967*

	Block	Nutrient level		
		LN	MN	HN
Predation level				
WF	I	6.25	11.99	1.38
	II	10.88	19.51	0.77
	III	14.03	11.31	4.45
F	I	45.66	26.16	0.25
	II	24.69	41.24	2.95
	III	8.13	20.60	5.07
Average		18.27	21.80	2.48
Control				
Pond 27:	15.31			
Pond 34:	26.85			

TABLE 26. Chironomus tentans *production (mg dry wt/232 cm²) from 14 June to 7 September 1967*

	Block	Nutrient level		
		LN	MN	HN
Predation level				
WF	I	248.12	638.02	318.71
	II	141.08	88.91	144.16
	III	371.19	444.32	122.01
F	I	74.08	200.99	451.90
	II	46.50	85.96	91.59
	III	169.18	484.52	159.08
Average		175.02	323.79	214.58
Control				
Pond 27:	55.88			
Pond 34:	80.07			

in Table 25. Estimates for LP and HP were 8.95 mg and 19.42. Both effects were significant ($P = 0.01$ and 0.05).

The effect of nutrient level on *Chironomus* production (Table 26) was not significant. The LN production increased each of the 3 years: 1965—88.17 mg, 1966—106.60 mg, 1967—175.02 mg. Production was highest in the MN ponds in 1967 and lowest in 1966. In HN ponds, 1967 was intermediate between 1965 and 1966. *Chironomus* production also showed no significant predation effect: Average production was 279.61 mg at LP and 195.98 mg at HP.

The net change in biomass standing crop during 1967 averaged 2.07 ± 4.61 ($\bar{x} \pm \text{SE}$) mg for all 20 ponds. This component was therefore not included in the production estimates. The average contribution of the mortality component was $82.9 \pm 2.6\%$ for all 20 ponds. In 1965 and 1966, mortality within the ponds contributed $65.5 \pm 7.9\%$ and $63.7 \pm 5.6\%$. Emergence contributed less to production in 1967 than in the preceding 2 years.

FISH

Methods

About 180 fish for stomach analyses were seined in the first weeks of June, July and August, equally distributed between ponds.

One population at each nutrient level (ponds 25, 26, and 35) was sampled in June; all ponds were included in July and August. Fish of comparable size from the holding ponds replaced those sampled. Young-of-the-year were caught throughout summer from the zooplankton samples and by dipnetting; these were preserved in formaldehyde.

The populations were harvested during the second week of September. Ponds were raked clear of macrophytes, and *Typha* sp. was removed from the edges to facilitate seining and to destroy any possible refuge. The ponds were then repeatedly seined. Consecutive hauls were made at right angles to each other until no more fish were caught. The fish were immediately preserved in formaldehyde.

Each pond was then treated with a rotenone solution mixed into the water column from a small pram with an outboard motor. In 10–15 min, convulsing fish appeared at the surface. Two crews seined constantly during this period. For the following week, the ponds were waded and the bottoms stirred to recover any remaining fish.

Each population was counted. The larger animals (those originally stocked) were measured to the nearest 0.5 mm. Young-of-the-year were separated into size categories, and subsamples were measured to provide size-frequency data. Length was taken as the distance from the tip of the snout to the anterior swelling of the hypural plate,
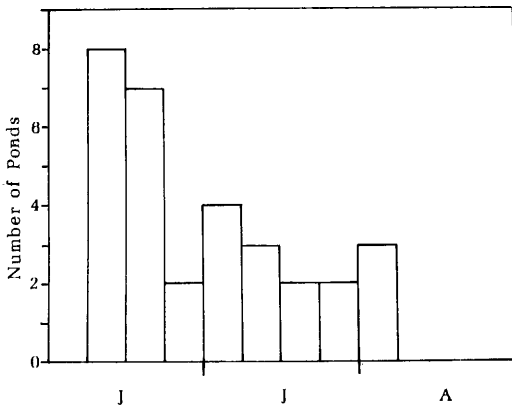
FIG. 80. Number of ponds containing an abundance of < 8-mm fry on the various sampling dates.

that is, standard length (about 78–80% of total length for the bluegill; conversion factors from Beckman 1945).

The fish were weighed after their weight had stabilized for at least 48 hr in forced draft ovens at 60C. Dry weight was uniformly 26% of the preserved wet weight (the weight of a specimen with excess moisture removed from the surface and all liquid drained from the coelom and air bladder).

Except for the subsamples, the entire cohort of young-of-the-year from each pond was dried by size categories. From total counts we could calculate mean individual weights for each category, and thus calculate the weight of those excluded for size-frequency measurements; these were then added to the total.

Samples of the stocked populations from each pond were dried and weighed. The samples ranged from 60 to 184 fish/pond, excluding class IV. Length–weight relationships were determined for both dry and wet weight to estimate population weights. The simple allometric formula $W = aL^b$ was used (W = weight, L = length, a is a fitted constant, and b the growth ratio). Data were fitted to a linear regression of the form: $\log W = \log a + b \log L$. Least squares estimates of parameter values and associated statistics were determined by computer analyses.

Results

Reproduction. Bluegills may carry from 3,000 to 19,000 ova, depending on the size of the individual (Ulrey, Rish, and Scott 1938). These hatch 2–5 days after fertilization as 1.3–3-mm prolarvae. By the 10th day, the yolk is absorbed and the 4.5-mm (std length) postlarvae leave the nest (Toetz 1966).

Large numbers of 4–8-mm fry appeared in the zooplankton samples on 14 June 1967 in all but pond 33; none had been collected previously. Evidently the fry were only vulnerable to the plankton net in this size range, as few larger than 9 mm were ever caught.

The distribution of fry in the samples indicated that reproduction continued during most of summer. Figure 80 gives the frequency distribution of ponds containing substantial numbers (25–90/tow) of 4–8-mm fry over the sampling period. (This information for individual ponds is presented in Fig. 81.) The sampling efficiency is unknown, so the data cannot be used for estimates of abundance, but they do indicate major recruitments into the populations.

Initial reproductive capacities of the various populations should have been similar as the fish came from common stocks and reproductive tissues had developed under identical nutritional regimes. Representative samples indicated that class IV and about 50% of class III (generally those > 65 mm long) carried mature gonads. Somewhat smaller individuals seined during summer were also mature.

Mean ($\pm$ SE) numbers of fry recovered in September from LN, MN, and HN ponds were 21,374 $\pm$ 3,293; 31,840 $\pm$ 6,230; and 25,098 $\pm$ 6,297. We have no evidence that nutrient level augmented reproductive activity.

Survival. Survivorship patterns in the young-of-the-year populations are unknown. Cohorts of fry recovered in the fall ranged from 12,712 to 43,702 per pond. This range could reflect differential mortality, varying numbers of successful broods in the individual ponds, or both. Total numbers of the
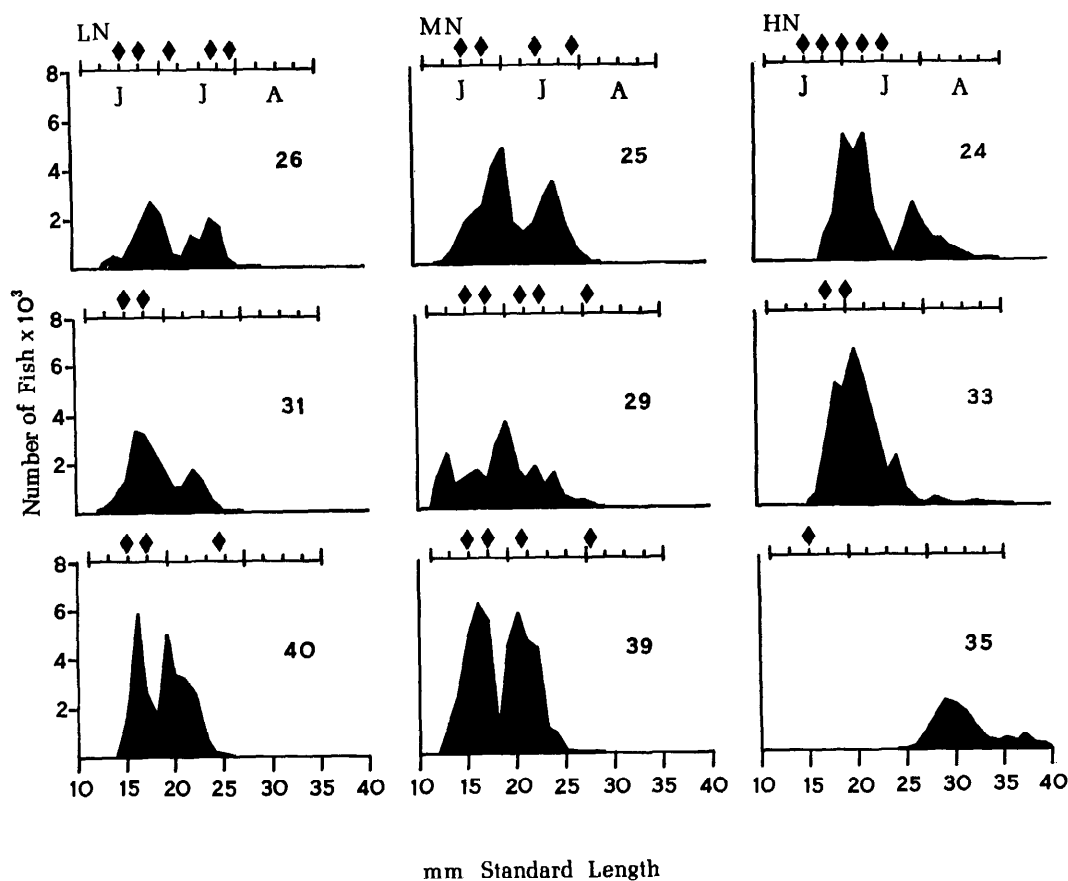
FIG. 81. Size-frequency distributions of the fry populations in September. The insert above each distribution is a time axis marked where major inputs of fry occurred.

stocked cohorts are available at the times the populations were introduced and killed (assuming complete removal). The size distributions of classes I, II, and III merged in the course of the summer's growth, obscuring the assignment of mortalities to these groups. Of the 1,250 fish stocked in classes I–III, 77–93% were recovered (Table 27), representing a mean percent survivorship (±SE) of 86.4 ± 1.26, 88.2 ± 3.52, and 85.4 ± 4.35 at LN, MN, and HN. There was no indication that nutrient level affected survivorship of these size classes. Recovery of class IV fish was complete in all ponds except 31 and 33, where 9 of the original 10 survived. Pond 29 contained 11 of this class due to a stocking error. Density is therefore eliminated as a con-

founding variable in the formulation of the initial stock's response.

Growth. Between 14 June and 2 August 1967, one to five major spawnings occurred in individual ponds, asynchronous after the initial pulse of 14 June. Figure 81 presents the timing of reproductive pulses, along with size-frequency distributions of the fry populations when harvested. In some of the ponds, reproductive pulses are correlated with peaks in the size-frequency distributions, particularly the initial pulse in June. Growth rates computed on this basis ranged from 0.13 to 0.28 mm in standard length per day, with the majority falling around 0.17 to 0.18 mm/day—values similar to others reported for bluegill young-of-the-year (Krumholz 1946; Lux 1960; Werner

TABLE 27. *Survivorship of the stocked* Lepomis macrochirus *populations*

Pond No.	No. recovered (classes I–III)	Initial cohort (%)	No. recovered (class IV)
24	959	76.7	10
25	1,019	81.5	10
26	1,098	87.8	10
29	1,168	93.4	11
31	1,094	87.5	9
33	1,132	90.6	9
35	1,110	88.8	10
39	1,121	89.7	10
40	1,049	83.9	10

TABLE 28. *Numbers and standing crop biomass of young-of-the-year* Lepomis macrochirus *populations*

Nutrient level	Pond No.	No. of fish	Dry wt biomass* (g)	Nutrient level mean (± SE)
LN	26	17,083	805	
	31	19,191	744	
	40	27,848	1,091	879.93 ± 107.13
MN	25	29,213	1,458	
	29	22,605	908	
	39	43,702	1,605	1,323.32 ± 212.24
IIN	24	29,310	2,237	
	33	33,273	1,797	
	35	12,712	3,206	2,413.09 ± 416.23

* 2.5% significance level.

1969). In general, growth rates were slightly higher at HN and varied inversely with the density of the associated cohort at any one nutrient level.

The sensitivity of these growth rates in adjusting the population to nutrient level and in compensating for numerical differences is indicated by the total dry weight of the fry populations in September (Table 28). Average standing crop biomass at MN was 150% and at HN 274% of that at LN. These are significantly different at the 0.025 level. The range over which this compensatory growth response can operate must be considerable. Pond 39 (MN), with 3.4 times the number of fry, had only 50% of the standing crop of pond 35 (HN). The growth response, in general, implies that the young-of-the-year are largely food limited and that the differences demonstrated between nutrient levels are not a function of the number of mouths available to capitalize on the pond's resources.

Although the numerical variance may not affect the biomass response the first year, it must certainly become important in subsequent seasons. Individual growth rates were retarded in the denser stocks and at lower nutrient levels. This effect would be compounded in future years by the slower progression to larger sized food particles (*see* p. 909) which can produce prominent bursts of growth (Parker and Larkin 1959). Future size and age distributions of these populations would likely be different.

There was no recruitment of fry into size classes associated with the initial popula-tions. Mortality in classes I–III averaged for all nutrient levels ranged from 13 to 15%. When September size-frequency distributions were plotted for each pond, those at any one nutrient level were practically congruent. Mortality in the populations appeared to be distributed in similar fashion, at least within treatment levels. A large portion of it probably took place early in spring as a result of incorrect handling during stocking. Production that was subsequently lost because of mortality was probably negligible or, in any case, relatively constant across ponds.

The initial and final size-frequency distributions of the stocked populations are given in Fig. 82. The original classes indicated by the histograms overlapped only slightly between II and III. Excluding class IV, the modal difference between HN and LN in fall is about 20 mm of standard length—a better than 3-fold difference in individual weight. As would be expected, higher growth rates tend to spread the distributions out somewhat.

Allometric equations for classes I–III were fitted to data from each pond by linear regression. The estimated tested parameters are given in Table 29. Using the technique of Ostle (1963), we tested the 9 regression equations and found they differed significantly. The data therefore were not pooled and biomass estimates for each pond were computed on the basis of regression parameters unique to that pond.

TABLE 29. *Estimated regression parameters for length–dry weight relationships of classes I–III (correlation coefficients were all 0.99)*

Nutrient level	Pond No.	Intercept	Slope	Sample size
LN	26	−5.58	3.28	124
	31	−5.65	3.31	60
	40	−5.45	3.20	185
MN	25	−5.61	3.30	105
	29	−5.69	3.35	69
	39	−5.54	3.26	93
HN	24	−5.66	3.34	74
	33	−5.77	3.40	70
	35	−5.62	3.32	74

Within each block, the slopes increase directly with nutrient level, indicating a condition factor (fish of a given length are heavier at higher nutrient levels). Estimates of mean dry weight biomass ($\pm$SE) are 1,795 ± 159; 2,773 ± 25; and 4,755 ± 415 g/pond at the three nutrient levels (Table 30). The response is remarkably uniform within treatment levels in view of the varying conditions in individual ponds. These classes, stocked at 357 g dry wt/pond, contributed most of the total population response.

Twelve of the class IV fish were recovered after poisoning, measured, and their weights estimated. The rest were handled directly in the usual manner. The mean length increment between nutrient levels of these fish is only 4–5 mm, but mean individual weights clearly show the nutrient effect (Table 31). These fish were approaching the limits of their growth form, at which proportionately more energy presumably would be channeled into fats and gonadal elaborations rather than to body dimensions. This would tend to in-

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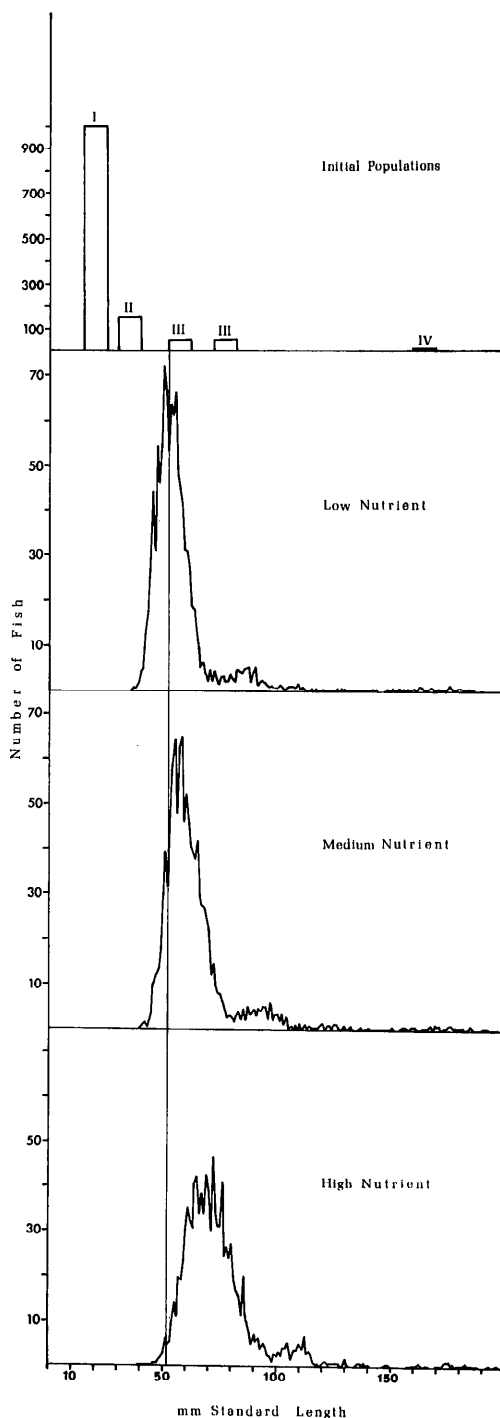
FIG. 82. Initial and resulting size-frequency distributions of the fish populations. The histograms are set on the modes of the original population structure (class III was equally distributed between two modes). The nutrient-level distributions are the means of three populations in September. Average standard errors over the primary mode are 3.68, 2.29, and 2.64 fish in LN, MN, and HN ponds.

TABLE 30. Lepomis macrochirus *standing crops of classes I–III*

Nutrient level	Pond No.	Total dry wt* (g)	Total wet wt (g)
LN	26	1,915	7,769
	31	1,989	7,559
	40	1,479	5,656
MN	25	2,813	11,109
	29	2,781	11,021
	39	2,726	10,888
HN	24	4,169	15,313
	33	4,539	16,885
	35	5,557	20,773

* 1% significance level.

TABLE 32. *Standing crops of* Pimephales promelas *in September*

Pond No.	No. of fish	Mean std length (mm ± SE)	Dry wt (g) Mean	Dry wt (g) Total
24	70	44.4 ± 0.4	0.29	21
25	1	57	—	—
26	161	49.1 ± 0.7	0.44	71
29	4	62.2 ± 1.3	—	—
31	363	44.0 ± 0.5	0.28	103
33	675	48.5 ± 0.7	0.43	288
35	207	53.6 ± 0.5	0.88	183
39	2	60.5 ± 0.4	—	—
40	—	—	—	—

crease the condition factor while minimizing length difference in treatment level comparisons.

The bluegill stocks from the hatchery were contaminated with the fathead minnow (*Pimephales promelas*). Although the fish were hand-sorted, a few minnows were accidentally introduced and managed to breed to varying degrees in ponds 24, 26, 31, 33, and 35. All other ponds contained negligible numbers of these fish (<5 individuals/pond). The fatheads were also measured, counted, and dried (Table 32). In no pond was the dry weight biomass of the minnows more than 4% of the weight of the bluegill population.

Guts of 120 fatheads (40 each from ponds 31, 33, and 35) were analyzed when the ponds were harvested in September. Less than 10% of these fish showed any evidence of invertebrates being taken and then only

one or two organisms per fish. All of the stomachs contained essentially detritus and lesser amounts of sand. Thus it seems unlikely that the fatheads were competing with the bluegills for a food source and were not affecting bluegill production directly at the densities present. For this reason we have excluded the fathead data from further production and population analyses.

When the standing crops of the various size classes are combined, a uniform response pattern is evident. At each nutrient level, the total population weight in fall is <85 g apart in two of the ponds (Table 33). Only ponds 29 and 35 extend treatment ranges more than 200 g. The pattern of response within the populations was also consistent. Figure 83 portrays the proportions of production attributable to stocked populations and to young-of-the-year. The

TABLE 31. Lepomis macrochirus *standing crops of class IV*

Nutrient level	Pond No.	Total dry wt* (g)	$\bar{x}$ dry wt (± SE)	$\bar{x}$ length (± SE)
LN	26	505	50.5 ± 3.72	165.1 ± 3.18
	31	491	54.5 ± 3.74	168.1 ± 3.29
	40	478	47.8 ± 3.17	165.1 ± 3.80
MN	25	634	63.5 ± 4.76	167.3 ± 2.79
	29	727	66.1 ± 2.97	176.6 ± 2.43
	39	658	65.8 ± 6.7	172.7 ± 3.98
HN	24	783	78.4 ± 5.89	176.0 ± 3.50
	33	807	80.7 ± 5.45	174.4 ± 2.57
	35	744	82.6 ± 7.50	177.3 ± 3.38

* 1% significance level.

TABLE 33. *Total population dry weight standing crops of* Lepomis macrochirus *in September*

Nutrient level	Pond No.	Dry wt* (g)	Increase over stocking rate (%)	Nutrient level mean % increase (± SE)
LN	26	3,226	378.36	
	31	3,223	378.11	
	40	3,048	357.59	371 ± 7.01
MN	25	4,905	575.37	
	29	4,416	518.00	
	39	4,989	585.26	560 ± 21.05
HN	24	7,189	843.31	
	33	7,143	837.87	
	35	9,507	1,115.15	932 ± 91.55

* 1% significance level.
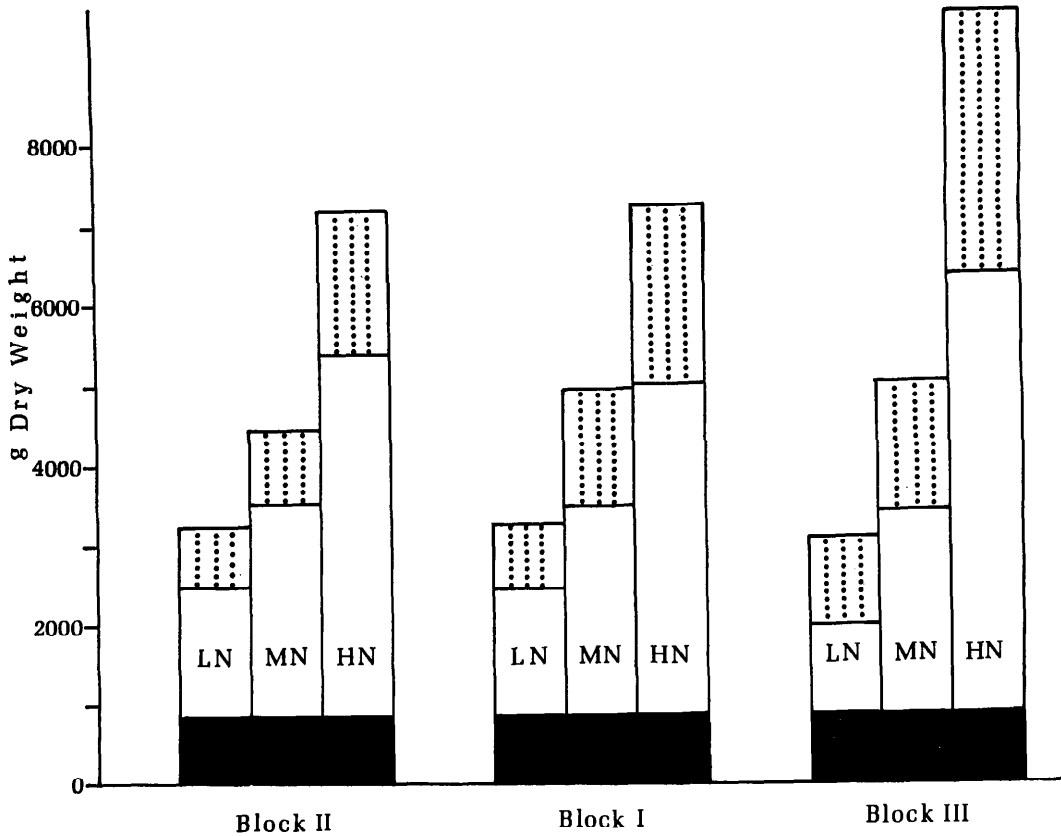
FIG. 83. Total standing crops in September divided into initial stock (solid), growth of the initial stock (blank), and young-of-the-year (dots).

proportion of the biomass elaborated (total dry wt − stocking rate) accounted for by the fry does not differ between nutrient levels (Table 34).

Individual growth is the dominant feature of the fish response. Initial numbers and weight, mortality in the stocked populations, and numbers of fry do not differ across treatments. Growth provided the adjustment to nutrient levels, resulting in a 3.6-fold to 11.2-fold increase in population dry weights. This response was predictable because the original populations were skewed to smaller individuals, but the data do serve to demonstrate the potential role that the plastic growth phenomenon can play in the population dynamics of fish.

Prey selection. Stomach contents were sorted and counted under a binocular microscope. Contents of 585 stomachs were examined: 218, 209, and 158 from LN, MN, and HN ponds. Sample sizes were fairly uniform for the three sampling dates, so no weighting procedure was needed. Organisms were generally identified to species except for midges, chydorids, copepods, ostracods, and halliplids. Species (or instars) were categorized according to size (cf. Tables 7 and 15). Table 35 lists the contribution of the various species to the categories as found in fish stomachs.

The fish were separated into 6 arbitrary size classes: 0–20-, 21–30-, 31–40-, 41–60-, 61–80-, and >80-mm standard length. The computer programs were written so that the number of prey organisms in each size or species category was summed for each fish size and printed out with the number

TABLE 34. *Proportion of seasons' growth accounted for by* Lepomis macrochirus *young-of-the-year*

Nutrient level	Pond No.	Total dry wt stocking rate (g)	Young-of-the-year (%)	Nutrient level mean % (± SE)
LN	26	2,373	33.92	
	31	2,371	31.36	
	40	2,196	49.69	38.33 ± 5.73
MN	25	4,053	35.97	
	29	3,563	25.47	
	39	4,137	38.80	33.41 ± 4.05
HN	24	6,337	35.30	
	33	6,290	28.56	
	35	8,654	37.04	33.64 ± 2.58
			Overall mean:	35.12 ± 2.30

of stomachs represented. On this basic format, analyses were performed across nutrient levels, individual ponds, dates, and various combinations of the above. Individual ponds within a nutrient level were strikingly similar in species composition so that further compilations were performed across nutrient levels. With the exception of a few species aberrations in time (e.g.,

D. pulex in June), which are accounted for below, dates within nutrient levels demonstrated the same trends with reference to particle size selectivity. The data were therefore combined across dates.

Fish size was important in the selection of prey items. This was evident from the species selected, but even more so when prey were classified by particle size. The number of prey items in each particle-size group summed for each size class of fish was divided by the sample size to reduce the data to the mean number of prey items per fish. These data are presented in a matrix of fish size against prey size for each nutrient level in Table 36. The strong diagonal aspect reflects the progressive selection of larger particles by the fish as they increase in size. The selection pattern is notably uniform for the three nutrient levels, in spite of the differences in composition of the communities. These two parameters seem to have considerable predictive import. Many nuances associated with species listings of gut contents and so on have largely obscured the more general pattern that emerges here.

TABLE 35. *Percent composition of the particle size classes found in the stomachs of* Lepomis macrochirus *across all ponds and dates*

	Particle size (mg dry wt)			
	A (>1.0)	B (1.0–0.1)	C (0.1–0.01)	D (0.01–0.001)
Midge pupae	43.8 (43.1)*			
Midge larvae	34.8 (21.2)	74.4 (72.7)	18.5 (17.5)	
Zygoptera	11.2 (24.0)	0.8 (0.7)		
Snails	9.4 (8.9)			
Dragonflies	0.4 (2.6)			
Hyalella		5.0 (1.6)	3.0 (1.9)	
Callibaetis		1.5 (2.6)		
Caenis		4.2 (3.7)		
Haliplidae		7.5 (9.9)		
Trichoptera		2.0 (3.4)		
Corixidae		3.1 (11.1)		
Dytiscidae		1.0 (1.1)		
Ostracoda			19.4 (5.1)	
Daphnia pulex			7.6 (6.3)	
Simocephalus			51.2 (69.1)	
Ceriodaphnia				1.9 (3.4)
Chydoridae				66.6 (57.3)
Bosmina				24.0 (20.7)
Copepoda				4.8 (16.7)
Rotifera				2.1 (0.9)

* Numerical percent composition (biomass percent composition).

TABLE 36.   *Mean numbers of particles per individual* Lepomis macrochirus

Nutrient level	Fish size (mm)	Particle size (mg dry wt)				Sample size
		A (>1.0)	B (1–0.1)	C (0.1–0.01)	D (0.01–0.001)	
LN	0–20	0.00	0.00	2.54	55.98	42
	21–30	0.03	0.50	8.29	72.21	28
	31–40	1.67	5.79	15.63	79.38*	24
	41–60	2.83	5.19	11.96	22.22*	103
	61–80	6.15	5.23	11.92	0.77	13
	>80	5.75	4.13	2.75	0.00	8
MN	0–20	0.00	0.02	2.41	48.92	61
	21–30	0.05	0.40	5.24	27.96	25
	31–40	3.57	6.36	12.07	2.93	14
	41–60	4.42	9.99	10.62	0.06	79
	61–80	9.09	8.04	11.09	0.13	23
	>80	7.29	2.29	9.57	0.00	7
HN	0–20	0.00	0.00	5.65	47.03	34
	21–30	0.00	0.24	16.05	141.17*	42
	31–40	1.44	0.67	30.78	66.67*	9
	41–60	2.83	5.98	64.51*	4.66	41
	61–80	7.83	7.04	92.39*	4.57	23
	>80	9.89	5.44	18.11	0.00	9

* *See text.*

Size of the fish and particle size of the prey are indicated as primary considerations in predation by bluegills. The data also suggest another significant parameter. Values that appear inordinately high relative to their position in the matrix are asterisked in Table 36; generally, these were larger fish selecting greater proportions of small particle sizes than expected. Data on individual ponds and dates were examined for possible contributing factors. In each case, these values could be explained in terms of high densities of a particular species. At LN, high values in category D are accounted for by high densities of *Bosmina* in June (see Fig. 23). At HN the asterisked values in the same size class relate the numerical response of *Chydorus* to nutrients (Fig. 22) in these ponds. Prey abundance is thus implicated as a third factor in predicting the distribution of particle sizes in the fish stomachs, and requisite prey size for a size class of fish might be modified to some extent by prey density.

The matrices also indicate the change during the ontogeny of the fish from planktophage to benthophage habit. Items found in the stomachs belonging to category D were exclusively planktonic forms (Table 35). Only three plankters, *S. serrulatus*, *D. pulex*, and Ostracoda, were large enough to be included in category C. *Simocephalus* was abundant only in HN ponds and *D. pulex* appeared only briefly in June. Ostracods were never abundant. Columns A, B, and C, then, consist almost entirely of benthic forms. In all cases, fish between 31- and 40-mm standard length began foraging on the benthos, corroborating the findings of Patriarche and Ball (1949). The smaller fish contained some prey in category C, but these were largely the plankters mentioned above. A few contained head capsules of larger midges but associated body parts were never found. It is not clear whether the fish were simply picking up head capsules or whether they were artifacts of differential retention times in the gut. After the switch to the benthos, the plankton quickly dropped out of the diet except in cases of extreme densities. If the values in Table 36 are converted to a biomass basis, the change is much more dramatic.

In summary, the size and stage of devel-

opment of the fish largely dictate its selection of prey. Prey size is certainly a primary consideration, although its density, activity, and vulnerability are also important. A shift from plankton to benthos takes place at a certain size during the fish's ontogeny. These patterns seem to be largely independent of considerable differences in the composition of the invertebrate community.

DISCUSSION

Zooplankton

Nutrients. Pond fertilization has been practiced for centuries and a wealth of empirical information exists, particularly with respect to maximizing fish production (Hickling 1962). But only recently have aquatic ecologists begun to design their experiments with pond systems more rigorously (Prowse 1968). Unfortunately, most studies have been concerned only with the correlation of fish yield to nutrient applications. Food chain dynamics and the role of zooplankton have been neglected except for the fundamental work on ponds done in Czechoslovakia and Poland (*see* Hrbáček and Novatna-Dvorakova 1965; Straškraba 1965; Grygierek, Hillbricht-Ilkowska, and Spodniewska 1967).

In our work on the effects of nutrients on secondary production, we tried to create three discrete nutrient conditions, the highest of which would fall short of ever creating anoxic conditions for the benthos. Our ponds were therefore enriched at a rate lower than in most studies aimed at maximizing fish production. Accordingly, our zooplankton standing crop values are somewhat lower than those reported in fishpond investigations.

Although the HN application resulted in the largest zooplankton biomass, the MN level did not always produce greater densities than the LN. We assumed that our nutrient input levels were equivalent to three discrete food levels for herbivores. There are obvious objections to this assumption: 1) The nutrient input levels may not result in significantly different nutrient concentrations in the ponds. The oxidized clay sediments can bind nutrients (espe-

cially phosphorus), and the phytoplankton-zooplankton response at HN levels may be due to saturation of this mechanism permitting an accumulation of nutrients in the water. 2) Plant production may not respond in a linear fashion to nutrient differences. 3) Plant production may not be equivalent to available food.

Chemical analyses indicated no differences between nutrient concentrations in LN and MN ponds except when the MN input was increased 3-fold in 1967. Phytoplankton production followed the same pattern. The HN ponds always exhibited significantly higher nutrient levels and phytoplankton production. Predictably, zooplankton standing crop and production increased only at HN levels.

Zooplankton production at each nutrient level over the 3-year period (Table 13) revealed only one marked change: a 100% increase in HN ponds in the third year. This change may have resulted from a gradual increase in the nutrient pool following the continued high-level fertilization of these ponds. But the rapid succession from a *Chara*-dominated benthic vegetation to either vascular plants or blue-green algae in HN ponds complicates any interpretation.

Maximum production of 7 of the 9 zooplankton species occurred in a different block each year: block II (1965), block III (1966), and block I (1967). By contrast, seasonal phytoplankton standing crop and productivity were highest in blocks I, II, and II for each year.

Not every zooplankton species responded positively to the HN level. Densities of *K. cochlearis* were drastically reduced under HN conditions when *Ceriodaphnia* was dominant; in 1967, with *Ceriodaphnia* reduced by fish predation, *Keratella* became abundant. Indeed, rotifers then contributed more than 25% of the zooplankton production. *Chydorus*, a cladoceran much smaller than *Ceriodaphnia*, responded in the same way.

Ceriodaphnia consistently accounted for >80% of the production in all ponds during the first 2 years and in all the ponds without fish in 1967 with one exception.

The contribution of *Ceriodaphnia* dropped from ~80% to <40% in HN ponds during the last 6 weeks of summer, coinciding with the maximum standing crops of macrophytes and blue-green algae. Apparently the larger *Ceriodaphnia* has a competitive advantage over smaller filter feeders in open water. This may be related to its efficiency in food gathering and utilization (Brooks and Dodson 1965). By contrast, at HN levels late in 1967 the macrophytes and blue-green algae provided a substratum for the more specialized sessile *Simocephalus* and *Chydorus*. Nutrient enrichment of the ponds, therefore, eventually resulted in a more diverse zooplankton community.

In general, the plankton community was characterized by temporal instability. Apparently, short-term changes in phytoplankton were associated with fluctuations in the zooplankton; these were most frequent in HN ponds. This phenomenon has been substantiated in a parallel set of ponds (O'Brien 1970). The characteristically short generation times of both components enhances the instability.

Regardless of nutrient level and other sources of variation, the proportion of *Ceriodaphnia* and rotifers remained similar the first two summers. Since food affects total zooplankton production, it probably also determines this consistent partitioning of production between components of the zooplankton community. Unfortunately there is little direct evidence to support this. Edmondson (1965) does point out that *Keratella* is probably restricted to smaller food particles (generally <10 μ) while *Polyarthra*, with a different feeding apparatus, feeds on larger particles (up to 35 μ). *Ceriodaphnia* is readily cultured on cells <15 μ. Based on the relationship of body length to size of food particle given by Burns (1968), the upper size limit of food for *Ceriodaphnia* should be about 20–25 μ. Different feeding habits may account for the differential response of these two rotifers in the presence of *Ceriodaphnia*. Experiments to examine such relationships could bring together the virtually dissociated production and competition approaches to community ecology.

Invertebrate predation. The literature on invertebrate zooplankton predators includes many species, primarily arthropods. Predatory zooplankters (*Leptodora*, *Polyphemus*, several cyclopoid copepods, *Asplanchna*, and *Chaoborus*) are often abundant. Fryer (1957) observed *Macrocyclops albidus*, *Cyclops vernalis*, and, to a lesser extent, *Mesocyclops leuckarti* to prey on rotifers and especially on crustacean zooplankters. *Chaoborus* can eliminate *Diaptomus shoshone* from alpine ponds (Sprules 1970); other studies show significant predation on the plankton by larvae of this insect. *Leptodora* (Cladocera) may consume significant fractions of the herbivorous zooplankton production (Cummins et al. 1969).

Many benthic predators also feed on zooplankton. However, only Johnson (1969) has quantitatively examined the predator-prey relations; he used experimental pools containing *Simocephalus* and the damselfly *Ischnura verticalus*.

Except for *Polyphemus* and *Leptodora*, all of the above predators lived in our ponds. But our manipulations involved only the hemipterans, odonates, and beetles. It was impossible to alter densities of the smaller predators.

The results reflect a quantitative effect of the insect predators on the zooplankton in both years at all nutrient levels, as shown by the percent difference in mean prey densities between HP and LP ponds (Fig. 18). We suggest size-selective predation, although the data are weak. In June 1966, *Daphnia* was strikingly reduced by predation (Fig. 15) while the smaller *Ceriodaphnia* were most abundant in HP ponds. After *Daphnia* disappeared, *Ceriodaphnia* populations declined. The HP pond densities of *Buenoa* and *Notonecta* seemed as great as any local, natural densities. We frequently observed notonectid and odonate cannibalism in the HP ponds. These two observations suggest that higher predator densities would not only be unrealistic, but could not be maintained.

Under some circumstances, then, invertebrate predation seems to have measurable but only slight effects on zooplankton production. Kaczynski (1970), in an experimental field study of the fairy shrimp *Eubranchipus bundyii*, concluded that predation (primarily by beetles) is far less important in determining population density than is food.

Several competition experiments have been performed in the laboratory with zooplankton (Frank 1952, 1957; Parker 1960, 1961). Burns (1968) has demonstrated the close relationship between maximum particle size ingested and body length of seven cladocera. More recently she has shown that filtering rates are primarily a function of body size, although strongly influenced by temperature (Burns 1969). None of these studies has been specifically designed to examine the ecological question of competitive success between filter feeders of different size experiencing various degrees of size-selective predation.

Fish predation. Much work has followed that of Hrbáček (1958, 1962), Hrbáček and Novatna-Dvorakova (1965), and Brooks and Dodson (1965) on the effect of fish predation on the composition of zooplankton. The theory of the regulatory role of fish predation can be stated as follows: As fish densities increase, the size of the dominant zooplankters decreases because of size-selective predation. The resulting community of numerous small zooplankton responds with comparable biomass production. Fish may increase nutrient turnover rates as well as remove larger prey species, but in the absence of fish the smaller zooplankton cannot dominate because of the higher grazing and processing efficiency of the larger zooplankton. Many quantitative, and often experimental, investigations on fishponds and backwaters (area, 0.02–31 ha) in Czechoslovakia and Poland have shown a surprisingly similar set of responses (Hrbáček 1958, 1962; Straškraba 1965; Gurzeda 1965; Grygierek et al. 1967; Hillbricht-Ilkowska 1966; Losos and Hetesa, in press). More descriptive but equally interesting results substantiating

the fish predation theory have come from larger water bodies (Brooks and Dodson 1965; Galbraith 1967; Brooks 1968).

Different fertilization levels should lead to quite different feeding situations for the bluegill fry which were the dominant planktivores in our ponds. At LN levels, the fish should demonstrate size selectivity more strongly (or more rapidly) than at higher nutrient levels. Our results confirm this. Table 14 shows smaller sized zooplankton in the presence of fish: 1) 90% *Bosmina* in LN-F ponds vs. 95% *Ceriodaphnia* in LN-WF ponds; 2) 36% *Bosmina*, 20% *Chydorus*, and 16% *Ceriodaphnia* in MN-F ponds vs. 97% *Ceriodaphnia* in MN-WF ponds; and 3) 39% *Chydorus* and 17% *Ceriodaphnia* in IIN-F ponds vs. 19% *Chydorus* and 44% *Ceriodaphnia* in HN-WF ponds. These trends follow those observed by Hrbáček (1962) and Grygierek (1962) and, as Hrbáček pointed out, cannot be explained by differences in pond productivity *per se*. Our *in situ* life table experiments during early August in ponds with fish resulted in large brood sizes (6–10 eggs), high birth rates, and good survivorship of *Ceriodaphnia* (Table 10). The profound reduction of *Ceriodaphnia* populations in our ponds with fish must reflect a direct predation effect rather than other environmental changes. These effects are quite apparent even at HN levels, where macrophytes partially confound the design (Fig. 34). The independent evidence from stomach analyses (*see* fish section) also supports the hypothesis of size-selective predation.

Whereas previous investigators have shown that fish predation is strongly size-selective (Hrbáček 1962; Hrbáček and Novatna-Dvorakova 1965; Brooks and Dodson 1965; Galbraith 1967), none has examined the interaction of prey size and density. In an experiment with alewives (*Alosa*), Brooks (1968) demonstrated a rapid shift in prey size selection from adult *Diaptomus minutus* through successively smaller life-history stages. However, all prey densities were equal. Fish will switch to the smallest zooplankters, but only after very

high densities are reached (Gurzeda 1965; Losos and Hetesa, in press).

The frequent dominance of natural zooplankton communities by small species may well be attributed to the prevalence of predation. Even in communities of species of the same size, selective predation may exert a strong effect. Zaret (1969) has shown prey selection to be a function of the relative size of the conspicuous compound eye of two *Ceriodaphnia* morphs of the same body size.

Experiments (Hrbáček 1962; Galbraith 1967) in which fish are removed (poisoned) from water bodies having zooplankton communities dominated by smaller species always produce a rapid shift to larger filter feeders. Re-examination of our 20 ponds in July 1969 (two summers following the fish experiment) showed that *Ceriodaphnia* was again the dominant plankter in all the former ponds that had fish, strengthening our conclusions regarding the effect of fish.

Rotifer densities increased at all nutrient levels under the influence of fish, with *K. cochlearis* and *K. hiemalis* invariably dominating—again corroborating the results of Hrbáček and of Grygierek. The highest densities were in HN ponds in late summer. Copepodids (both calanoid and cyclopoid) also contributed a larger percentage to the zooplankton biomass in ponds with fish. Adults were rare. Again, this may represent a secondary, compensatory response to the removal of *Ceriodaphnia* by fish.

Although fish drastically affect community composition and species production of zooplankters, other factors must regulate total production at HN levels to the degree that species composition is irrelevant. Food is the most likely factor, since nearly all herbivorous zooplankters feed on a rather narrow range of the available particle sizes and, as discussed above, nutrient levels appear to strongly influence zooplankton production. We did not observe any difference in phytoplankton chlorophyll *a* concentrations or ^{14}C assimilation between ponds with and without fish, so similar zooplankton production might be anticipated. We need more extensive data on the magnitude, size fractions, and availability of food production to critically evaluate this point.

Fish predation affected the structure of the zooplankton community more acutely than did invertebrate predation; it is unlikely that this comparison is an artifact of our selection of densities. Invertebrate predator densities were probably maximal in HP ponds. Young-of-the-year bluegills recovered in September spanned a 4-fold density range; yet in each pond the result of fish predation was equally striking. Our estimate of the impact of fish is probably realistic. Our observations confirm the predictions of Holling (1965) that vertebrates are more effective predators than are invertebrates.

Benthos

Nutrients. The importance of benthos to fish production has often been stressed, but there have been few careful analyses of the effects of nutrients on the dynamics of benthic populations. Presumably such effects can be mediated through changes in either the quantity or quality of food available to the benthos (Jónasson 1969). Kajak (1960, 1963, 1964, 1965) designed a series of experiments to test the effect of food quantity on macrobenthos. Available food was manipulated by additions of organic material and by altering population density. Food supplements increased both the density of Chironomidae and individual growth rates (Kajak 1965), but increased densities of *Chironomus plumosus* adversely affected both population and individual responses of the smaller benthic species: *Chironomus anthracinus, Microtendipes, Procladius,* and *Valvate* (Kajak 1963). The inverse relationship between the dominant large midge *C. plumosus* and smaller benthic forms is similar to the *Chironomus–Caenis* response we observed. However, Kajak's experiments were continued for only 1 month.

Eisenberg (1966) changed adult densities and food quality of the snail *Lymnea elodes* in a replicated design. Augmenting

natural food with a small amount of high quality food (spinach) resulted in a 25-fold increase in the number of eggs produced and a 4-fold increase in numbers of young snails. The food supplement produced a more striking response than that from a 25-fold increase in adult densities. Cooper (1965) found that although densities of *H. azteca* fluctuated significantly in the field, brood sizes did not change. The number of eggs per brood observed in the field was less than half that produced by females of similar size in the laboratory. Again, food quality appeared to be the limiting factor.

Our nutrient additions, which resulted in significant responses by the dominant benthic organisms, produced both quantitative and qualitative changes in food. Possible mechanisms for the observed differences, however, may be inferred from the feeding behavior of these animals.

In 1965, the standing crop biomass of the benthos increased in proportion to the fertilization regime. Most of this biomass consisted of *C. tentans*, especially in the HN ponds. This organism has a short generation time (14–30 days), is very fecund (about 2,500 eggs), and was the largest benthic omnivore (up to 2 mg dry wt). During daylight, *Chironomus* feeds extensively on plankton by filtering out small particles on a silk web constructed within tubes in the sediment; the respiratory and feeding mechanisms are both dependent on the circulation of water through these tubes. The animals pump by body undulations which cease periodically while ingestion takes place. At night, *Chironomus* searches the sediment surface adjacent to the tube for the larger food items. These two modes of feeding enable it to use both plankton and benthos, and its large size permits a wide range of food items. *Chironomus* can thus quickly capitalize on the initial production responses to nutrient addition.

Caenis simulans on the other hand responded inversely to nutrient addition. *Caenis* is a small omnivore (<0.8 mg dry wt), having only 2 generations/year. It cannot filter feed and consumes a restricted size range of food particles (Brown 1960). The *Caenis* populations in HN ponds could be reduced by physiological intolerance to the environmental conditions, predation by large *Chironomus*, replacement of edible epiphytes by coarse filamentous algae, or competition with young *Chironomus*. The population data indicate that, whatever the mechanisms, the responsive stage was early in the life cycle. The most likely explanations are either antagonistic effects of *Chironomus* or inadequate food for the smallest instars (Brown 1960).

By mid-1966, the increasing dominance of *E. canadensis* and *Potamogeton* sp. in HN ponds apparently was imposing constraints on the development of the benthos, which had shifted from large sediment dwellers toward small mobile forms that browse on epiphytes. This shift was independent of predation and was associated with increased stratification of the water column, decreased light penetration (thereby reducing production of benthic algae), and reduced concentrations of plankton immediately above the sediments during daylight. Whatever the processes involved, the shift to mobile grazers reapportions benthic production rates so that the plankton is no longer a dominant food input. The change in primary producers from filamentous benthic algae to macrophytes may further reduce the available food supply. All these factors probably interact to reapportion benthic production in HN ponds.

The total benthic biomass at LN levels during the 3 years was remarkably constant (avg, 20–40 mg/sample). Total biomass at MN levels declined between 1965 and 1966; an increase in 1967 was caused by the 3-fold increase in nutrient addition. Total standing crops at HN levels declined sharply following spring emergence in 1966 and remained relatively low the following year.

In these freshwater ecosystems, enrichment alone is not sufficient to maintain maximum standing crops of benthos; a periodic disruption of normal vegetation development is also necessary. This, of course,

is the reason for the practice in most fish-pond management of draining ponds for short periods between fish crops. It aerates the soil, inhibits development of stable macrophyte populations, and maintains a benthic community with maximum production potential.

The benthic communities in our ponds were apparently not unusual; their traditional measures fall well within the ranges in the literature. Numerical densities were between those given by Kajak (1966) and Jónasson (1961) for natural lakes and similar to those in fertilized ponds (Patriarche and Ball 1949; Ball and Tanner 1951). Standing crop biomasses ranged up to 5.2 g/m²; reported values fall between 0.42 and 12.4 g/m² (Ball 1949; Buscemi 1961; Gerking 1962; McIntire and Bond 1960). The production estimates available are also of the same magnitude as ours (Anderson and Hooper 1956; Gerking 1962; Cooper 1965; Waters 1966; Kajak 1967).

Invertebrate predation. Several workers have reported the general trophic relationships of benthic invertebrates from the analyses of gut contents (Walshe 1951; Brown 1960; Chutter 1961; Corbet 1962; Pritchard 1964; Cummins, Coffman, and Roff 1966). None of these studies has evaluated the impact of this predation on the prey populations.

Anax junius was the major benthic predator that we manipulated. It is a large visual feeder with crepuscular activity. Ross (1967) found that *Anax* in our ponds fed primarily on large, active prey, especially third and fourth instar *C. tentans*. The only other organism eaten in quantity was late instar *Caenis.*

The invertebrate predators had no consistent effect on the total benthic biomass; their effects only became apparent when the benthic fauna was partitioned by species or body size. Holling (1965) reported a negatively accelerating (type 2) functional response curve for several aquatic invertebrate predators (*Lethocerus, Notonecta, Acilius*). He predicted that when functional response alone is considered, invertebrate predators will be less able to

control abundances of prey populations than are vertebrate predators. We manipulated the numerical responses of *Anax* to produce very low and extremely high predator densities. At lower nutrient levels, the invertebrate predation was sufficient to influence the *Chironomus* populations, particularly through later instars. The corresponding increase in *Caenis*, however, masks any predation effect when both prey are combined in a total biomass analysis.

Fish predation. Studies of the relationship between fish predation and benthic production have most often been descriptive, using correlations with fertilization (Ball 1949; Patriarche and Ball 1949), fish densities (Gurzeda 1965), fish production (Gerking 1962), and invertebrate production (Borutsky 1939; Buscemi 1961; Momot 1967; Cooper 1965). Experiments with temporal changes in fish abundance (Ball and Hayne 1952; Hayne and Ball 1956; Macan 1966) and artificial exclosures (Lellak 1957, 1966; Kajak 1966; Berglund 1968) provide more rigorous control. None of these studies has yielded a substantial picture of the relationship between benthic dynamics and fish predation; the descriptive ones were not designed to test specific hypotheses, and the experimental manipulations either were unreplicated and confounded in time or their results were dominated by the effects of artificial exclosures.

We found that fish predation, like invertebrate predation, had no effect on the total benthic biomass; such a composite parameter will obviously hide component interactions that are inversely related. But the interaction component indicated a consistent predation effect at LN levels.

The biomass of emergent insects showed the most consistent predation effect of all community parameters. Ponds with fish produced fewer emergent insects than those without fish at all three nutrient levels. The difference in predation effect on larval and adult biomass was a result of the strong selection of insect pupae by bluegills. The fish, by eating large, abundant particles, were selectively removing the

terminal aquatic stages of many benthic insects. The intensity of this selection is demonstrated by the fact that insect emergence in ponds with fish did not increase with food levels. In ponds lacking fish, it increased significantly at HN levels.

Chironomus tentans, Zygoptera, and *Hyalella* were most preyed upon. *Chironomus* was reduced in ponds with fish at all three food levels, almost entirely by losses in the third and fourth instar larvae and pupae. The standing crops of Zygoptera in ponds with fish were a tenth of those in ponds without fish at all three nutrient levels. Fish predation also inhibited late summer increase of *Hyalella* populations at LN and MN levels. All of these benthic organisms are large, mobile, and often abundant.

Community. Aquatic predators apparently select prey primarily on the basis of size (Holling 1965, 1966; Brooks and Dodson 1965; Galbraith 1967), and aquatic herbivores may show the same type of restriction in their food (Brown 1960). Most aquatic organisms thus do not recognize their food as taxonomic entities nor as members of a trophic level; food consumption is a function of particle size, availability, palatability, and abundance. Many organisms, especially predators, consume the largest particle sizes that they can manage.

As expected, then, the most consistent response to our manipulation of nutrients and predator density was apparent in the analysis by body size, which ignores behavioral, taxonomic, and trophic characteristics, but nevertheless appears to be one of the most informative abstractions of the benthic community structure. The usual community analyses, based on taxonomic or trophic criteria, are probably most relevant to evolutionary phenomena. The short-time community responses of our study were better characterized by changes in the distribution of body size.

Another pattern emerging from consideration of body size concerns the spatial distribution of benthic organisms. Ivlev (1961) has demonstrated the importance of prey distribution with reference to fish predation. In our system a predator with a small perceptual field which selects large prey (like *A. junius*) will encounter a relatively low density and highly dispersed distribution of prey in LN ponds; in HN ponds, its probability of encountering dense clumps of large prey is much greater. As the macrophyte populations develop in HN ponds, the large prey particles become more uniformly distributed. Predators that select small prey items (*Procladius, Ablabesmyia*) will encounter a wide range of prey densities with equal probability in LN ponds; in HN ponds, a more uniform distribution and a lower density of small particles of prey will be available. Nutrients, then, may have an important effect on the strategy of predation in the system.

It is evident that the composition of the littoral benthic community was affected by both nutrient and predator manipulations, but the patterns of community response were not stable with time. The effect of sustained nutrient input at HN levels on total production decreased over the 3-year period. Superimposed on this were changes in species and their relative abundance; in the more highly structured plant communities (*Chara, Potamogeton, Elodea*), small animals dominated, although larger animals flourished in the filamentous algae communities. Control ponds showed essentially no change during the 3 years. The mechanisms responsible for these patterns in community development probably involve both the physical complexity provided by the benthic vegetation and the partitioning of primary productivity between palatable and unpalatable plant forms. Predation resulted in similar responses in species distribution: Large animals were heavily preyed upon, permitting compensatory increases in small organisms. Of the two parameters, nutrients had the most pronounced effect on production. However, this was a relatively short-term effect following the initial step input. Both nutrients and predation have a long-term influence on the species composition of the benthos.

Fish

Population response. Fish have an indeterminant growth pattern; growth potential, maturation, and senility are more a function of size-related physiology than of chronological age (Brown 1957). There is evidence for this plastic growth in reference to food, density, and competition (Beckman 1941; Ball and Tanner 1951; Backiel and LeCren 1967; Hepher 1967).

Our study illustrates the role of growth in the population dynamics of fish. Most fish production was in the form of growth of the stocked population; mortality was relatively constant. The young-of-the-year displayed a spectrum of growth responses relating nutrient and density factors. Numbers of fry harvested from the ponds differed with vagaries in reproduction or mortality—a common pattern in fish populations. Recruitment into the population seldom is related to the adult stock (Ricker 1958) and mortality remains relatively constant over the larger size classes. Growth, then, appears the parameter most sensitive to environmental conditions and adjusts the population's biomass. McFadden and Cooper (1964) and McFadden, Cooper, and Andersen (1965) also found this pattern in stream salmonids.

The inverse relationship between density and individual growth may affect the size distribution of the population. A dense pulse of fry may stunt in a particular size class, skewing the size distribution. But food habits often change during ontogeny, so the growth of the rest of the population may be relatively unaffected. The retardation of individual growth in an abundant cohort may be further compounded in those size ranges where the fish switch to larger particles or from the plankton to benthos. Parker and Larkin (1959) have shown that bursts of growth can occur here. This may have happened in pond 35 where the fry came off the nests as a single cohort. The mode of the September distribution was at about 30-mm length (*see* Fig. 81). The distribution was positively skewed to 45 mm, although the figure is arbitrarily truncated at 40 mm. We have shown that the
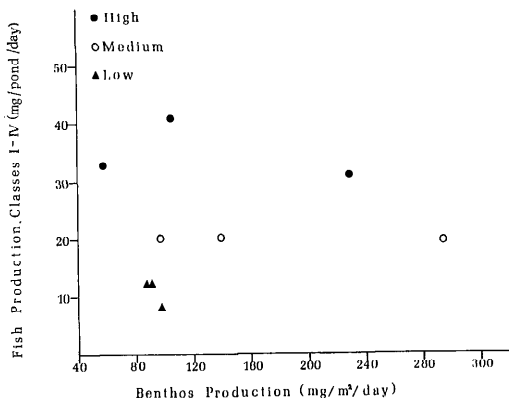

FIG. 84. Benthos production vs. production of the stocked population for individual ponds at three nutrient levels.

fry switch to eating benthos between 31 and 40 mm. Increased growth rates after the switch to a new food source of larger particle size may account for the attenuated positive tail.

Our data indicate some of the responses of fish populations to their environment, but they cannot answer questions of long-term effects. The responses evoked in the population are intimately tied to the stochastic elements in reproduction, the size structure of the population, overwintering conditions, competition, and so forth. This type of study must be extended over more than one season.

Production. The distribution of fish production across nutrient levels showed the clearest, most consistent response. The addition of inorganic nutrients increased this production predictably. Although component or total herbivore production in individual ponds deviated considerably from the expected pattern, the fish production in no case fell out of line (Fig. 83).

In the ponds with fish, benthic production was highest at MN. Most of the biomass consumed by the stocked fish was benthos (Tables 35 and 36), so we expected a correlation between benthic and fish production but did not find one (Fig. 84). *Chironomus tentans* constituted the largest part of the diet, but plotting this
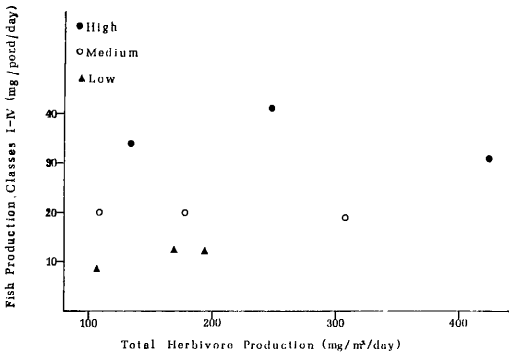
FIG. 85. Total herbivore production vs. production of the stocked population for individual ponds at three nutrient levels.

TABLE 37. *Mean standing crops of particles in the benthos from 21 May to 7 September for the ponds with fish. Data are No./Ekman dredge*

Nutrient level	Pond No.	Particle size (mg dry wt)			
		A (>1.0)	B (1.0–0.1)	C (0.1–0.01)	D (0.01–0.001)
LN	26	4.08	10.88	137.50	120.58
	31	1.83	11.54	158.58	180.17
	40	2.58	9.50	99.04	154.21
MN	25	13.13	24.54	182.63	165.71
	29	11.46	30.04	167.33	141.42
	39	15.29	37.46	239.08	316.21
HN	24	5.92	18.63	91.46	64.33
	33	10.21	22.79	53.33	53.75
	35	15.99	34.46	91.04	119.71

component against fish production did not improve the relationship.

The ability of the fish to turn to zooplankton as food under conditions of high prey density could compensate for vicissitudes in benthic production. When production of the benthos and zooplankton are combined, the means across nutrient levels indicate a trend to higher production with nutrient input. The individual ponds, however, vary so greatly that within blocks the relationship is not at all clear. In block II the LNF pond was the most productive, while in block III the MNF pond was highest. These values are plotted against fish production in Fig. 85; again, there is no correlation. The addition of fry production, which was based on the zooplankton, will not change the relationship because it was nearly a constant proportion of total fish production across all nutrient levels.

The lack of any correlations indicated that we were not working with the appropriate aspect of herbivore (= prey) production. Except in the few cases noted, the stomach analyses depicted a consistent pattern of particle size selection across nutrient levels (Table 36). The relative proportions of benthos in the categories of body size, however, differed with nutrient level, though not as markedly in 1967 as in previous years. This was also true of the zooplankton, as evidenced by the species composition (Fig. 33). We tentatively concluded that the fish did not select particles

relative to their abundance in the environment and, therefore, that the availability of requisite size particles may be the governing factor.

To test this hypothesis, we computed mean standing crops of particles in the benthos for individual ponds with fish (Table 37). No benthos <0.01 mg dry wt was found in the fish stomachs, so category D can be excluded from the analyses. Those remaining constitute the overwhelming portion (biomass) of the diet of the stocked population over the season (class I may have been temporarily planktivorous in the spring). The average numerical standing crop for categories A and B was always smallest at LN and nearly the same at MN and HN—the same pattern as in the stomach contents (Table 36). Category C increased from LN to MN and decreased considerably at HN, but the pattern in the stomachs was the opposite. To measure the contribution of these classes more accurately, we computed weighted means of the dry weights of animals in the guts for categories A–C. Multiplying these factors by the mean number of particles of that size in the fish stomachs gives an idea of the relative contribution of that particle size to the biomass of the diet. For fish >31 mm long, category C contributed 4% at LN, 3% at MN, and 13% at HN. Except in pond 24, categories A and B do not differ between MN and HN either in the stom-

achs or in the environment. At HN the diet is apparently supplemented by category C.

Category C in the benthos of HN ponds was relatively rare; its increase in the fish stomachs was due to *Simocephalus*. To see how much *Simocephalus* would expand the HN values in Table 37, we computed mean standing crops from 7 July to 30 August on the basis of the dip-jar samples, which are representative of populations in the macrophytes. The net samples had indicated that *Simocephalus* was at least as abundant before 7 July as after. It was abundant only in HN ponds (Fig. 33), averaging 58, 102, and 112 adults/liter in ponds 24, 33, and 35. We calculated numbers of adults only, since the majority in the stomachs were large, egg-bearing individuals. To obtain numbers on an areal basis comparable to that for the benthos, we computed the volume of water for a stratum 0.6 m over the bottom inside the sloped edges, multiplied this by numbers of *Simocephalus*/liter, and divided by the number of Eckman dredge units in this bottom area. This yields the number of *Simocephalus* over an Eckman dredge unit in an arbitrary 0.6-m column of water that approximates the mean height occupied by macrophytes. The mean number of adult *Simocephalus* per column in ponds 24, 33, and 35 are 821, 1,444, and 1,586. These estimates may vary to some extent depending on density of the macrophyte cover, but certainly are of the correct order of magnitude.

This means of calculation greatly expanded category C at HN. Summing across A–C gives the average standing crop over the summer of requisite particles available in the environment, and these show a marked relationship to standing crop of the stocked fish (Fig. 86). The abundance of large particles seems to provide the margin of difference in fish production. Converting the figures to a production basis would involve largely linear factors and the relationship would not be altered significantly. This is obviously true of the fish; only *Simocephalus* production would require ad-
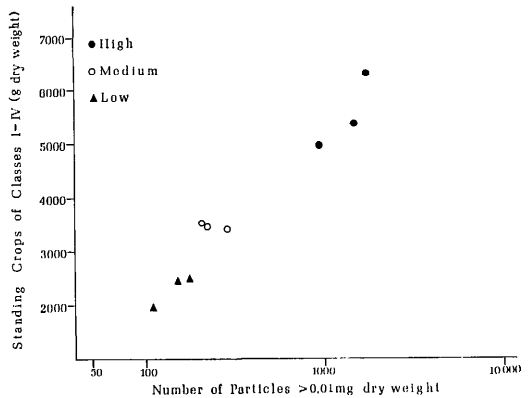

FIG. 86. Summer mean standing crops of particles >0.01 mg vs. standing crop of the stocked population in individual ponds at three nutrient levels.

justment, as the rest of the particles are benthos of roughly comparable generation times.

We cannot as yet make a more quantitative statement of the relationship. Obviously the addition of *Simocephalus* at HN distorts it somewhat; the contribution of this animal in the stomachs is much lower than its abundance in the environment would suggest. *Simocephalus* occupies the dense macrophyte beds exclusively, spending a large proportion of its time attached to the weeds. Its habitat and low activity, coupled with small body size, seem to reduce its vulnerability to fish predation. A correction for availability based on these factors would bring the HN points in Fig. 86 back in line with the steeper slope of the LN and MN values. On the other hand, the abundance of larger particles may be underestimated at HN, since a significant portion of the benthos probably occurred on the weeds in these ponds and the Eckman dredge does not sample the weeds nearly as well as the sediments. Pond 24 especially was choked with *Elodea*, probably explaining the lower estimate of large benthos here (Table 37). This qualification is critical because these larger particles are responsible for most of the biomass consumed. Also, benthic animals, particularly those in the >1 mg category, generally

represent larger particles at HN levels than at the lower nutrient levels. Several larger species in the benthos at HN were lumped in the "others" category. These differences plus the 10% increase in biomass in the stomachs due to *Simocephalus*, prorated by some metabolic efficiency, would be incorporated by the population each day (digestive times for the bluegill are given by Windell 1967). If integrated over the course of summer, these differences would certainly account for the additional production at HN. This is, of course, evidenced at LN and MN where small differences in average standing crop of prey are plotted against the integration of these differences by the fish over the growing season (Fig. 86).

The evidence strongly suggests that fish production is directly related to the production of a subset of the larger invertebrates in the ponds and may have no bearing on total herbivore production in the community. The reasons for which this is such a consistent and stepwise response to nutrient input are not at all clear. There is some indication that increased nutrient levels select for larger body size in the herbivores, particularly in the benthos and in the early stages of a nutrient flush or succession (e.g., note the practice of fallowing fishponds in Europe). Increasing the nutrient input at MN in 1967 evoked this response. The physical matrix (macrophytes) in the ponds also seemed important, but unfortunately in our system the weeds could not be separated from the HN level. The provision of a refuge by the weeds apparently permits an array of larger species to exist in the presence of fish which may in turn provide for greater fish production. These two factors will have to be pulled apart before we can understand the community dynamics.

Prey selection. Most studies of the feeding of fishes have attempted to document the general food habits of various species so they can be placed in the trophic scheme. A few relate the dynamics of the fish stock to its food organisms (Allen 1951; Gerking 1962) or the effect of fish

predation to the dynamics of the prey (Hayne and Ball 1956; Hrbáček et al. 1961; Straškraba 1965; Galbraith 1967). A number of questions concerning the mechanisms of fish predation have been experimentally approached by Ivlev (1961). This information has led to interesting inferences, but the piecemeal nature of its accrual has not permitted a unified picture to develop. The predators and their prey community have seldom been followed simultaneously in a fashion adequate to delineate the nature of the interaction.

By attempting this type of study in ponds we hoped to elucidate phenomena of more general ecological import. The bluegill feeds by sight on a wide variety of aquatic invertebrates; all animals except those buried in the sediments would presumably be to some degree available. Only oligochaetes and nematodes were found deep in the substrates; there was no indication of these in the stomachs. Availability should be a function of the position and behavior of the animal (i.e., activity). We have no measure of availability, although inferences are possible from the habitat of the animal, knowledge of its behavior, and incidence in the fish stomachs relative to the particle size selection patterns. Several studies on the food habits of bluegills (Gerking 1962; Keast 1965; Ball 1948; Leonard 1940) show that their diet changes from zooplankton to one dominated by insect larvae as the fish grow. Werner (1969) has shown in Crane Lake, Indiana, that the pelagic fry return to the littoral zone at about 22–25 mm long; presumably they would begin feeding on littoral benthic fauna. Patriarche and Ball (1949) found a marked change in diet from entomostracans to midges in young-of-the-year bluegills around 40 mm (std length).

A few major factors seem to determine the nature of fish predation in our study. The size and ontogeny of the fish dictated their selection of prey; regardless of nutrient level we found fish between 31 and 40 mm (std length) switching to benthic prey. Even at very low zooplankton production, fish smaller than 31 mm did not

forage the benthos where small particles were abundant. Superimposed on the switch to the benthos is the general trend to larger prey in direct relation to fish size. This is well documented in the matrices of Table 36. This relationship remained intact despite changes in the species composition and size distribution of particles at the three nutrient levels.

Several interactions serve to modify this basic model. Primarily, density interacts with particle size to modify selection, so that larger fish will select small particles above certain densities. A related factor is the vulnerability of the prey organism; fish will exploit much smaller items when they are in exposed conditions (e.g., pelagic zooplankters). Under such conditions, actual species extinctions took place. Benthos of <0.01 mg dry wt that live in or on the substrate, although very abundant, were not found in fish of any size. The density-vulnerability factor, then, may explain why all deviations in the original matrices can be accounted for by zooplankters. The switch to the benthos seems to be a distinct life-history phenomenon; an interaction of factors in the environment can, however, induce facultative planktivory, to an extent probably dependent on whether the plankter is pelagic or littoral.

It is possible at this point to comment on the strategy that a generalized aquatic predator, typified by the bluegill, might use to procure food. The evidence suggests that the predator's prey gestalt depends upon parameters such as body size, activity, and density rather than any form of species preference. Adding the vulnerability factor allows us to describe an efficient predation process. We can reasonably expect that the thresholds are so built into this system that it would be an energetically profitable proposition. As the fish become larger they must take larger particles for maintenance and growth. Only if smaller particles are very abundant does it become efficient to feed on them. This is also conditional on the position of a particular density of small organisms in a gradient from open water to a dense phys-

ical matrix (i.e., macrophyte beds). In open water, particles larger than rotifers are a worthwhile investment (i.e., the annihilation of Ceriodaphnia), and particles the size of Bosmina can exist in an intermediate physical matrix (our LN and MN ponds); large particles can exist in a dense matrix (Simocephalus in macrophyte beds at HN). It may be that an interaction between fish predation, complexity of the physical matrix, and the hypothesis of body size efficiency (Brooks and Dodson 1965) in the competition between zooplankters operates to structure these communities.

When absolute densities of organisms are quite high, another type of response becomes evident. At HN, where this was common, most of the fish were specialists. Tinbergen (1960) and Holling (1965) have suggested that such a response is a conditioning or learning phenomenon that increases searching efficiency. At lower food levels, the fish stomachs contained a relatively diversified assemblage of species despite the unchanging constraints of the particle size selection. This type of feeding in the long run could be more inefficient and may contribute to differences in fish production.

GENERAL DISCUSSION

A prime motivation of this study was our experience, having followed single species in the field, that only limited inferences about aquatic communities could be made from such data. Indeed, the important questions concerning the forces that structure the aquatic animal community were not at all clear. We felt, however, that changes in species populations needed to be related to each other and followed simultaneously through time and that plankton and benthos interact and needed to be studied in concert. An overview such as this would then provide direction toward those factors that organize species populations in these communities and toward other emergent properties. It is difficult to piece this sort of picture together from the literature because of the wide range of conditions and because field data are

most often collected from small-scale studies unrelated in time or space.

By manipulating community structure and following its dynamics through time, we have found consistent patterns of response that appear to be of considerable ecological import. The analysis of these data is by no means complete; more can be done with community parameters, the population analyses of species other than dominants, and so forth. The initial analysis, however, indicates areas that seem to merit more detailed and functionally oriented investigations and that corroborate important contemporary work in ecology. We will here try to outline some of these ideas in a more general context than before.

Two of the major organizing processes in an aquatic community are competition and predation. Working on the rocky intertidal community, Paine (1966, 1969) has delineated the interaction of these forces. By manipulating a starfish population, he demonstrated that its predation on the dominant prey organism reduces competition for space to the point that other species become conspicuous in the community. He called this predator a "keystone" species. When such a species is high in the trophic web, it can influence the nature and extent of interactions among a whole subweb of species; thus considerations of diversity and stability in the community are inextricably related to the characteristics of the keystone predator.

The bluegill appeared to play much the same role in our system. Diversity increased under the influence of fish. New species appeared (particularly in the zooplankton) but, even more strikingly, the equitability between species increased throughout. Depredation of the large dominants allowed a marked complementary response of smaller species (Caenis, Rotifera, etc.). Apparently, as in Paine's system, the predator is inhibiting expression of the otherwise strong competitive advantage of the dominant species. We, however, have no direct evidence of the commodities around which this competition operates. Food is by inference most likely,

especially in the relatively simplified habitat of the zooplankton. We were generally able to increase production in both the zooplankton and benthos by nutrient additions, and there appeared to be compensation in production by smaller animals so that in terms of total production no predation effect was evident in either community. Such observations imply that food was providing a strong limiting constraint to these populations.

Both our results and those of Paine indicate that communities, or perhaps subsets of species in a community, may be held relatively stable by the forces of competition between species. If one or a few resources of fairly uniform quality are of preeminent competitive importance (space, food), then just a few species will dominate the community. A predator may hold such a community stable in a completely different form with respect to species and their relative abundances. Here the coactive forces have been largely replaced by predation as a major process in maintaining the structure of the community. Of course, any point on the continuum between these extremes may prevail in a given natural system.

There are parallels in the nature of the predators so important to these two systems. Both bluegills and starfish are large and mobile with respect to the prey assemblage. They are of fairly general trophic habit and thereby capable of exerting a direct effect on an extensive subsystem of prey. Both predators apparently select the larger prey when available: In Paine's system, Pisaster preferentially feeds on the mussel, Mytilus; in our system, the bluegills select the vulnerable Ceriodaphnia in the zooplankton and C. tentans in the benthos. These are all dominant animals in the communities in the absence of predation. The broad-scale effects of the predator, of course, are a function of its preference for these dominants. Its ability to switch to other prey species as they become more abundant, however, is imperative to its contribution to community stability (Elton 1927). The prey selection of Pisaster has

been discussed in terms of a species preference hierarchy (Paine 1969; Landenberger 1968). We need not evoke this type of argument in our system where a relatively stable preference system is constructed around particle size, not species. The interaction of size and density can result in a sort of switching of attention to expanding species populations. If this interpretation were true of predators in general it would simplify construction of a quantitative theory.

Another property that these two predators have in common is a marked capacity for indeterminant growth. This enables the predator population to functionally respond to prey density by shunting energy into plastic growth. Accordingly the predation effect on the prey populations is released to some extent from the major time lags introduced by a numerical response. The predator population biomass is thus tightly coupled to the prey system, providing a more stable predator–prey balance. *Pisaster* merely shrinks in the face of food shortage (Paine, personal communication); fish have a remarkable ability to shut down their catabolism to bridge troughs in food abundance. This permits the integration over time of variances in prey populations— an important component of stability in the system. The predators, by switching between prey species and by indeterminant growth, can react to, and maintain a balance among, constituent prey populations, in effect regulating the nature of their interactions.

The predator apparently need not be a major energy transducer in the community to manifest this sort of control. With emphasis on larger prey sizes, the reproductive individuals are probably quite vulnerable, and relatively small energy transfers could thus affect the prey population significantly. The breadth of the predators' effect on the community can also be attributed in part to their ultimate body size relative to the distribution of body size of their possible prey. The effect of fish on the zooplankton, for instance, would not have been nearly as great in the absence of fry,

while the larger size classes could handle the largest invertebrates in the ponds.

Of course, the actual situation is more complex than this, and the nature and extent of the environmental structure will qualify the argument. The importance of environmental heterogeneity is certainly not a recent revelation, but its critical role is clearly shown in these two systems. According to Paine (1969), the large-scale coexistence of *Mytilus* and *Balanus*, both preferred prey of *Pisaster*, is only possible where growth, reproduction, and recruitment take place in refuges from *Pisaster*. In our system likewise the effects of predation on the zooplankton inhabiting the open water were dramatically different from those on the zooplankton restricted to the bottom or to macrophyte beds. The larger benthic species, also preferred prey, are less vulnerable because they live among sediments or weeds. Their early instars are essentially free from fish predation since fish small enough to concentrate on this particle size seem to be largely planktivorous. Even when the small benthos were quite dense, larger fish did not switch to them, as they did to increasing densities of zooplankton in the same size range; this again is probably related to habitat complexity. It has been argued that increased environmental structure ameliorates competition: It is quite possible in this case that competition is enhanced by environmental structure, to the extent that the weed matrix affords protection from fish predation. These three interacting factors, predation, competition, and environmental heterogeneity, need to be studied in combination.

It is difficult to relate nutrients or production in any substantial fashion to the argument above. With regard to production our aquatic animal communities appear remarkably flexible in the sense that complementary responses were the rule in both the zooplankton and benthos. Nutrients certainly affect the benthic community both directly in terms of production and indirectly in controlling species or body size. The response of the zooplankton was
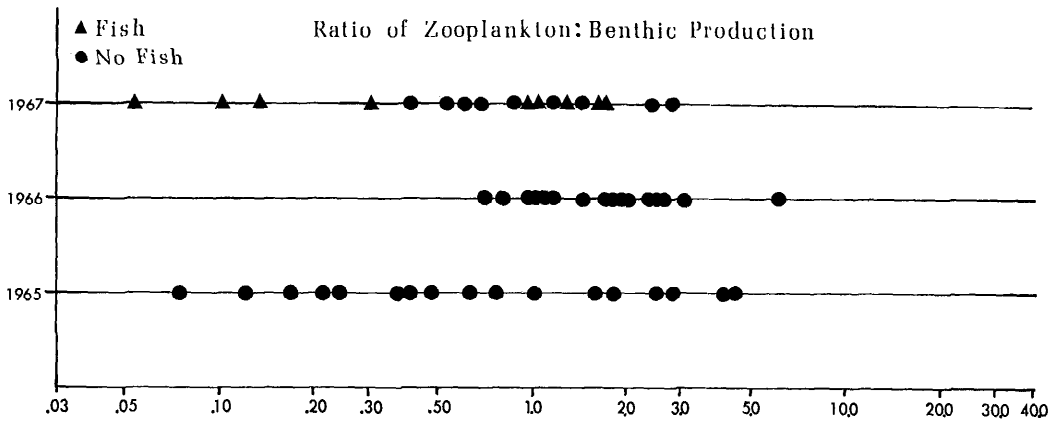
FIG. 87.   Ratios of zooplankton to benthic production for 18 ponds over 3 years.

essentially an increase in production without changes in species or equitability.

Our initial step input of nutrients drastically affected a whole set of species interactions—especially at HN. In a short time the benthic flora and fauna were completely restructured. The ubiquitous *Chara* was quickly replaced by filamentous algae and the invertebrates shifted accordingly. This same sort of phenomenon occurred in 1967 when the MN level was raised 3-fold. When subjected to a steady rate of nutrient input this community appeared to stabilize in the sense that production, variance, and biomass decreased while species numbers and equitability increased. Variations in nutrient addition, both in timing and amount, maintained the system in an unsteady state. This form of disruption inhibits the stabilization of relationships between the components of the system. These arguments, of course, are isomorphic with those on an evolutionary scale concerning the unpredictability of the environment.

There are other indications that the stress of initially changing the baseline nutrient levels upsets the community structure. This was found in regard to the relationship between zooplankton and benthic production. Since most of the zooplankton and benthos consume the same general food types (phytoplankton, detritus, bacteria, epiphytes), we thought it possible that the same sort of compensation could occur be-

tween these two communities as took place within them. The ratios of zooplankton and benthos production may also suggest general patterns in the coupling of the two communities. We calculated Z:B ratios for each pond all 3 years. Zooplankton production was calculated for a 1.3-m column above 1 m^2 of substrate, with a 2-fold correction factor for sampling bias (*see* methods). Benthic production was estimated directly for *C. tentans*, *C. simulans*, and Zygoptera from standing biomass. These production estimates were scaled up to include all the benthos by applying *Caenis* production rates (mg m^{-2} day^{-1}) to the remaining miscellaneous biomass; we used *Caenis* because the other benthic organisms have similar generation times. In general, the corrected benthos estimates were not much larger than the sum of the *Chironomus* and *Caenis* production.

These ratios averaged slightly greater than unity all 3 years (Fig. 87), indicating that production was somehow held roughly equal in the two communities. We can offer no *a priori* reasons why this should be so, yet two-thirds of the 54 ratios were close to one. The distribution of the ratios shifts from a negative skew (low values predominate) in 1965 to a normal, compact curve in 1966. In 1967, the ratios are again skewed toward low values, with the lowest values associated with ponds having fish at MN or LN levels. The changing pattern

could be interpreted as a reflection of highly varied responses to initial fertilization (stress), followed by a stabilized distribution of secondary production ratios in spite of continued nutrient input, then disrupted by the selective predation pressure of fish and increased (3×) nutrient input to MN level ponds. Further studies should be directed at the possible coupling mechanisms between these two communities under both disruptive and more stabilized conditions.

We are optimistic about approaching such questions by experimentation at the ecosystem level. Extending manipulation to the whole system in the field, of course, involves a considerable loss of control and compounds the traditional problems of statistically screening responses in biological data. We need fresh insight into the parameters that are most meaningful to measure at this level. Precision should be enhanced by more appropriate choices of parameters at higher levels of organization, as we found with body size. Nevertheless, the strength of the approach resides primarily in its systematic alteration of community and ecosystem level phenomena. From such broad-level manipulation, theoreticians should gain perspective on the proper choice of assumptions from which to construct ecological theory, and the experimentally or descriptively oriented investigator should receive fruitful direction to the myriad cause and effect relations requiring empirical attention. To bring these schools to a common ground of problems and approaches is, at this time, of utmost concern to the advancement of ecology.

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